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Edited by
Rob Barrett   John Cooper   Tony Gaston

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MARINE ORNITHOLOGY

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SYMPOSIUM

SEABIRD BIOGEOGRAPHY: THE PAST, PRESENT, AND FUTURE OF MARINE BIRD COMMUNITIES

GUEST EDITORS:
K. David Hyrenbach and David B. Irons

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INTRODUCTION TO THE SYMPOSIUM ON SEABIRD BIOGEOGRAPHY: THE PAST, PRESENT, AND FUTURE OF MARINE BIRD COMMUNITIES

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INTRODUCTION

> *"Overhead the albatross*
> *Hangs motionless upon the air*
> *And deep beneath the rolling waves*
> *In labyrinths of coral caves*
> *An echo of a distant time*
> *Comes willowing across the sand*
> *And everything is green and submarine.*
> *And no one called us to the land*
> *And no one knows the where's or why's.*
> *Something stirs and something tries*
> *Starts to climb toward the light."*
> *Echoes*, Pink Floyd, EMI Music 1971

The extreme life-histories of seabirds have long captured the imagination of artists and scientists alike. Recently, technological and conceptual advances have revolutionized the way researchers approach the study of seabird ecology and biogeography. Developments in the fields of genetics, wildlife telemetry, remote sensing, and geo-informatics; a growing appreciation of large-scale oceanographic patterns; and the compilation of long-term physical and biological time series have contributed to opening a window into the previously unknown habits of these majestic long-distance travelers.

Increasingly, marine ornithologists are adopting a broader approach to understand how oceanographic variability, changes in marine food-webs, and human activities affect seabirds over multiple spatial and temporal scales. Inter-disciplinary studies of seabird populations and communities have highlighted the important role these upper trophic-level predators play in marine ecosystems, and have enhanced the general understanding of biogeographic and ecological processes in the global ocean (Aebischer *et al*. 1990, Ballance *et al*. 1997, Veit *et al*. 1997, Hunt *et al*. 1999).

In addition to enhancing the understanding of marine biogeography and biotic responses to changing ocean climate, marine ornithologists can provide valuable insights into the management and conservation of entire ocean ecosystems. The value of marine birds as indicators of changing ocean productivity patterns and ecosystem structure is becoming increasingly apparent, as studies continue to document their sensitivity to fluctuations in pelagic food-webs, prey availability, and ocean climate (Montevecchi & Myers 1995, Furness & Camphuysen 1997, Kitaysky *et al*. 2000, Sydeman *et al*. 2001).

In particular, seabirds are increasingly being used to sample the physical and biological properties of the marine environment in real-time (Wilson *et al*. 2002). For instance, the movements and diving activity of individual foragers have been used to infer prey resource distributions and to ground-truth oceanographic conditions during periods (e.g., winter) and in locations (e.g., Southern Ocean) difficult to sample synoptically by more conventional means (Kooyman *et al*. 1992, Weimerskirch *et al*. 1995). These "biological sensors" will likely become an integral part of the developing Global Ocean Observing System (Block *et al*. 2002).

The study of seabird ecology is increasingly motivated by evidence that bird populations globally are being affected by human activities (Piatt *et al*. 1990, Croxall 1998, Tasker *et al*. 2000). In particular, an understanding of seabird distributions and habitats has important conservation implications. First, the accurate determination of population numbers at sea is essential to determine the status of rare and endangered species that are difficult to census at breeding colonies (Spear *et al*. 1995, Woehler 1996). Accurate population trends are urgently needed because mounting evidence suggests that many species are being impacted by anthropogenic activities (Wooller *et al*. 1992, Tasker *et al*. 2000) and are declining precipitously (Croxall 1998, Lyver *et al*. 1999). Secondly, an understanding of important foraging areas and migratory routes is essential for implementing large-scale conservation measures such as fishery closures and Marine Protected Areas (MPAs), (Boersma & Parrish 1999, Hyrenbach *et al*. 2000).

SYMPOSIUM SUMMARY

At the 30th annual meeting of the Pacific Seabird Group (19 - 22 February, 2003) held in Parksville, British Columbia, we convened a symposium to review the status of marine bird biogeography and to provide recommendations for further study. Eighteen oral papers, addressing a wide range of patterns and processes ranging from 10s to 1000s km and from weeks to centuries, were presented. Throughout this review, we will refer to these papers using the name of the first contributor. The eighteen symposium presentations are listed below, in alphabetic order:

ALLEN, S.G., & SCHIROKAUER, D. Keep it simple – selection criteria of marine protected areas for seabirds.

BADUINI, C.L. Biogeography of foraging strategies among Procellariiform seabirds: How productivity in surrounding waters influences foraging.

BURGER, A.E. Effects of the Juan de Fuca Eddy and upwelling on seabirds off southwest Vancouver Island, British Columbia.

DAVOREN, G.K., MONTEVECCHI, W.A. & ANDERSON, J.T. Distribution patterns of Common Murres *Uria aalge*: Underlying behavioural mechanisms in the context of predator-prey theory.

FORD, R.G., AINLEY, D.G., CASEY, J., KEIPER, C., SPEAR, L. & BALLANCE, L.T biogeographic analysis of seabird distributional data from central California.

HAAS, T. & PARRISH, J.K. Resolving fine-scale environmental patterns using beached bird surveys.

HATCH, S.A. & GILL, V.A. Geographic variation in Pacific Northern Fulmars: Are there two subspecies?

HIMES-BOOR, G.K., FORD, R.G., REED, N.A., DAVIS, J.N., HENKEL, L.A. & KEITT, B. Predictability of seabird distributions within the Gulf of Farallones at various temporal and spatial scales.

HYRENBACH, K.D. Marine bird response to interannual oceanographic variability in a dynamic transition zone: Southern California (1997-99).

KULETZ, K.J., BRENNEMAN K.M., LABUNSKI, E.A. & STEPHENSEN, S.W. Changes in distribution and abundance of Kittlitz's Murrelets relative to glacial recession in Prince William Sound, Alaska.

MORGAN, K.H. Oceanographic variability and seabird response off the British Columbia coast, 1996-2002.

PIATT, J.F. & SPRINGER, A.M. Biogeography of the northern Bering and Chukchi Sea shelf.

PITMAN, R.L., BALLANCE, L.T. & HODDER, J. Physiographic island evolution as a factor structuring seabird communities: Evidence from a temperate and a tropical setting.

SMITH, J.L. & HYRENBACH, K.D. Galapagos to B.C.: Seabird communities along a 7,800 km transect from the tropical to the subarctic eastern Pacific Ocean.

STEEVES, T.E., ANDERSON, D.J. & FRIESEN, V.L. Phylogeography of Sula: The role of physical and non-physical barriers to gene flow in the diversification of low latitude seabirds.

STEPHENSEN, S.W. & IRONS, D.B. A comparison of seabird colonies in the Bering Sea and Gulf of Alaska.

WILLIAMS, J.C., KONYUKHOV, N.B. & BYRD, G.V. Human influences on whiskered Auklet distribution and abundance through time.

YEN, P.P., SYDEMAN, W.J. & HYRENBACH, K.D. Bathymetric associations underlying marine bird and mammal dispersion in central California.

The symposium illustrated the cross-section of inter-disciplinary research approaches currently used to relate seabird distributions to prey dispersion, environmental variability, and anthropogenic impacts. The most prevalent topic addressed at the symposium was the relationship between seabird at-sea distributions and oceanographic variability (Burger, Davoren, Ford, Haas, Himes, Hyrenbach, Morgan, Piatt, Smith, Yen). Ten papers discussed changes in seabird communities with respect to water mass distributions and productivity domains over a broad range of spatial and temporal scales. Smith related the composition of seabird communities to oceanographic conditions along a 7,800 km spring-time transect across the tropical – subarctic Northeast Pacific Ocean, and documented three distinct assemblages associated with distinct water masses, defined by sea surface temperature and chlorophyll concentration. Two other presentations described seasonal and interannual changes in seabird communities off British Columbia (along a 1,500 km transect across the Northeast Subarctic Gyre; Morgan), and off southern California (grid of 6 survey lines, spanning from the coastline up to 700 km offshore; Hyrenbach) during the 1997-98 El Niño and the 1998-99 La Niña events. These large-scale studies confirmed that distinct seabird assemblages inhabit different water masses, characterized by specific physical (e.g., sea surface temperature) and ocean productivity (e.g., chlorophyll concentration) patterns. As the use of voluntary observing ships (VOS) expands, the capability to repeatedly survey marine bird distributions over basin-wide spatial scales will increase. A particularly exciting and pioneering research venue entails the integration of marine bird surveys and continuous plankton recorder (CPR) data along a 7,000 km east-west transect from B.C. to Japan (Sydeman *et al*. 2003).

Two other presentations focused on seabird associations with smaller-scale bathymetric (e.g., shelf-breaks, seamounts), and hydrographic (e.g., eddies, coastal upwelling) habitat features. Burger described year-round seabird distributions off SW Vancouver Island with respect to sea surface temperature and bathymetry, and highlighted the aggregation of these predators within an area of strong upwelling associated with the edge of the Juan de Fuca Canyon. Yen analyzed the spring-time (May – June) associations between marine bird distributions and bathymetric habitats in the Gulf of the Farallones, central California, and reported substantial variability in seabird habitat use patterns across weeks (repeated sweeps within a survey) and across years (different spring cruises between 1996 and 2002). Together, these papers reinforced the often well-defined association of seabirds with specific ocean habitats over multiple spatial scales, ranging from the large-scale dynamic hydrography (e.g., water masses, 1000s km) to the small-scale bathymetry (e.g., shelf-breaks and canyons, 10s km).

Five synthetic presentations illustrated the biogeographic and management applications of time series of marine bird distribution and abundance patterns (Allen, Ford, Himes, Kuletz, Piatt). Piatt's discussion of the biogeography of the northern Bering and Chukchi Sea shelf related the habitat preferences of different seabird foraging guilds (piscivores and planktivores) to physical (e.g., water column mixing) and biological (e.g., ocean productivity) regimes. Himes addressed the predictability of marine bird distributions within the Gulf of the Farallones, central California, over a wide range of temporal (24 hours – 6 months) and spatial (1 – 100 nm^2) scales. The paper by Ford provided an example of an applied biogeographic assessment of individual marine bird species dispersion and community composition (e.g., overall density and biomass, species diversity) off central California, conducted in support of the National Marine Sanctuary management plan review. Kuletz's presentation highlighted the value of long standardized time series to detect climatic impacts on seabird populations. Between 1972 and 2000, Kuletz documented a 85-95% decline in Kittlitz's Murrelet *Brachyramphus brevirostris* abundance in Prince William Sound, Alaska, linked with the retreat of glaciers in the area.

Two presentations explicitly addressed steps for the design of marine zoning strategies to protect important seabird habitats (Allen, Davoren). Allen proposed a framework for delineating Marine Protected Areas (MPAs) for seabirds, including (i) ecological (e.g., species rarity, diversity, sink-source dynamics), (ii) sociological (e.g., commercial and sport-fishing effort), and (iii) regulatory (e.g., jurisdiction, existing designations, enforcement capabilities) criteria. An alternative route to MPA designation was presented by Davoren, who used repeated vessel-based visual and hydro-acoustic surveys to delineate "habitat hotspots" of predictable predator (Common Murre *Uria aalge*) and prey (capelin *Mallotus villosus*) aggregations off Newfoundland, Canada.

Several studies examined how prey influenced seabird distribution and abundance patterns over a variety of spatial and temporal scales (Baduini, Burger, Davoren, Kuletz, Piatt, Stephensen). Piatt and Stephensen invoked ocean productivity patterns and prey transport and retention mechanisms to explain the disparity between breeding seabird populations within different bathymetric domains of the Bering Sea and the Gulf of Alaska. Baduini investigated how large-scale (100s – 1000s km) ocean productivity patterns influence the foraging strategies of Procellariiform (tubenose) seabirds, and proposed several hypotheses to explain the alternation of long and short foraging trips observed in many of these far-ranging species. Burger, Kuletz and Davoren pointed out the significance of prey distributions and availability, as determinants of seabird distributions at smaller (10s – 100s km) spatial scales. Additionally, Davoren emphasized the importance of previous experience (e.g., remembering where predictable prey patches are located), and local enhancement (e.g., locating prey patches by cueing on conspecifics at sea). These presentations raised two particularly exciting concepts that deserve additional study: the reliance of foraging birds on memory and the fidelity to specific foraging areas.

In addition to habitat-use considerations (e.g., oceanographic conditions, prey dispersion) known to influence seabird distributions over hours – decades, several papers addressed biogeographic determinants operating over longer ecological – evolutionary time scales. Stephensen and Williams highlighted the impacts of humans on seabird breeding populations since the 1700s, through the introduction of predators to subarctic islands. Two other presentations discussed the influence of geomorphology on the density and the distribution of seabird breeding populations. Stephensen ascribed some of the differences in seabird breeding populations in the Aleutians and the Gulf of Alaska to geographic disparities in the extent and type of volcanic soil. A novel presentation by Pitman described the influence of changing island physiography on the structure of breeding seabird communities.

The symposium also highlighted novel techniques and approaches to the study of marine bird biogeography, including genetics, morphometrics, and satellite telemetry. Baduini reviewed the value of telemetry to study the foraging behavior of far-ranging seabirds. Steeves showcased the value of genetic techniques to study seabird speciation. Her paper discussed the role of physical and non-physical gene flow barriers as factors inhibiting the diversification of low latitude seabirds. Hatch reviewed the patterns of geographic variation in Northern Fulmars *Fulmarus glacialis,* prompting the question of the existence of yet to be identified subspecies. Haas illustrated the potential of long-term monitoring programs as sources of valuable ecological data. The Coastal Observation and Seabird Survey Team (COASST), a beached bird survey in Oregon and Washington, is a prime example of the novel approaches being used to involve volunteers in seabird research. In addition to monitoring potential die-off events, these programs provide valuable specimens for genetics, morphometrics, and contaminant studies.

FUTURE AVENUES AND OPPORTUNITIES

Maintaining and expanding existing time series

A pervasive take home message from many of the symposium presentations was the recognition of the inherent difficulties associated with documenting long-term changes in biological communities. Temporal trends are difficult to quantify because they require a series of repeated standardized surveys, and long-term data archiving. Both the field sampling and data management components of monitoring programs are expensive, and difficult to support with the existing framework of 3-4 year funding cycles. Fortunately, visionary researchers had the foresight to start various marine bird population time series several decades ago. Today, these data sets provide a priceless historical perspective necessary to interpret present conditions and to forecast the future. These observations, which become more valuable every year, constitute one of the most precious resources at our disposal. As inferred by several of the symposium presentations, the true value of long time series is only apparent after major regime shifts and population changes. In anticipation of future oceanographic variability (e.g., ENSO, PDO), climate change (e.g., global warming, glacial recession), and potential anthropogenic impacts (e.g., oil spills, fisheries bycatch, exotic predator introductions) maintaining and expanding the coverage of existing time series is a main research priority.

Ideally, existing long-term monitoring programs will be enhanced with short-term hypotheses-driven studies aimed at elucidating the mechanisms underlying specific patterns or observations. Previously, short-term studies have shown how seabird assemblages quickly respond to shifting physical characteristics (e.g., water mass distributions), and that these changes can be non-linear, with variable magnitude and direction (Hyrenbach, Morgan). However, little is understood about how these short-term population responses to oceanographic variability (e.g., redistribution during an El Niño event) translate into population-level changes (e.g., survivorship and reproductive success).

Previous studies have clearly substantiated the notion that marine bird assemblages are not fixed in space and time, but are susceptible to changes in water mass distributions, ocean productivity, and prey availability. However, it is also recognized that species-specific differences in life-history and ecology influence the habitat associations and the responses of individual bird species to environmental change. Thus, a better understanding of how different biotic and abiotic factors influence the susceptibility of certain populations and species to climatic and anthropogenic impacts is essential to forecast the fate of marine bird communities. This improved knowledge will require comparative studies involving large data sets spanning a broad geographic and taxonomic scope.

Promoting inter-disciplinary research

Future seabird biogeography research will be inextricably linked to the study of climate change and anthropogenic impacts. The increasing awareness of the importance of the underlying oceanographic variability has promoted a multi-scale understanding of the ecology of marine birds (e.g., Hunt & Schneider 1987). This integrative perspective should be enhanced in the future, by integrating marine birds within broader oceanographic research programs. In particular, three interrelated aspects deserve additional study: (i) how ocean productivity affects the distribution and aggregation of prey; (ii) how prey dispersion influences the distribution, prey selection, and foraging effort of seabirds; and (iii) whether enhanced foraging effort impacts the reproductive success and survivorship of seabird populations.

The widely recognized patterns of climatic variability in the Pacific Ocean underscore future opportunities to investigate the response of seabird populations to changing ocean climate across the globe. Analyses of global ocean temperature since the beginning of the 20th century have revealed three dominant regimes of climate variability in the North Pacific: (i) a progressive temperature increase associated with global warming, (ii) 20-30 year periods or “regimes” of alternating warm and cold water conditions termed the Pacific Decadal Oscillation (PDO), and (iii) shorter 1-2 year warm (El Niño) and cold (La Niña) water periods linked to the El Niño Southern Oscillation (ENSO) (Mantua *et al*. 1997, Folland *et al*. 1999, Levitus *et al*. 2000).

The long-term warming trend has been linked with drastic changes in the physical structure of North Pacific temperate and subpolar marine ecosystems since the 1950s (McGowan *et al*. 1998, Arendt *et al*. 2002, Bograd & Lynn 2003). Yet, little is known about potential synergies between this long-term variability and higher frequency fluctuations associated with shorter-term ENSO and PDO oscillations. Understanding the coupling of high (i.e., ENSO) and low (i.e., PDO) frequency environmental variability, and the influence of these phenomena on future global warming trends will require continued time series of physical and biological properties. These data will be essential to interpret and forecast changes in marine ecosystem constituents (McGowan 1990, McGowan *et al*. 1998).

Because anthropogenic impacts in the global ocean are pervasive, marine ornithologists must also consider changes in seabird prey availability, foraging effort, reproductive success, and mortality caused by human activities (e.g., overfishing, oil spills, introduced predators, bycatch). As the fields of oceanography, climate change, and ocean conservation merge, marine ornithologists will find themselves at an inter-disciplinary cross-roads (Hyrenbach *et al*. 2000, Ainley 2002, Block *et al*. 2003). This integrative science will be founded on international collaboration, multi-disciplinary research, and the creation of “data commons” for standardization and sharing of information.

Creating a Data Management Infrastructure

The same way atmospheric scientists and oceanographers have amassed long-term databases of physical and biological variability, efforts are underway to compile global distribution and abundance data for several marine taxa. These initiatives are driven by large-scale biogeographic studies, and by efforts to better manage protected species and marine ecosystems. The Ocean Biogeographic Information System (OBIS), a bio-informatics initiative under the auspices of the Census of Marine Life (CoML) and the U.S. National Oceanographic Partnership Program (NOPP), has initiated several projects to characterize global species distributions and biogeographic patterns for a broad array of marine taxa, ranging from hexacorals to seabirds (Decker & O’Dor 2002).

In addition to these biogeographic initiatives, a rapidly growing number of conservation programs are compiling databases of species distribution and abundance to guide the management of protected taxa (e.g., Procellariiform tracking database), to delineate important marine habitats (e.g., Patagonian Shelf project), and to facilitate the design of networks of Marine Protected Areas (Bering to Baja initiative).

Biogeographic data on North Pacific seabirds are currently being compiled in three regional archives: North Pacific Seabird Colony Database, North Pacific Seabird Monitoring Database, and the North Pacific Pelagic Seabird Database. These databases will include distribution and abundance data, spanning from the equator to the pole along both sides of the basin. The colony database, being managed by the U.S. Fish and Wildlife Service in Anchorage, contains information on nesting sites of colonial seabirds, including species, numbers, and locations. The monitoring database, to be managed by P.S.G., U.S.G.S. and U.S.F.W.S., includes many different colonial seabird population and productivity parameters, which have been measured repeatedly to allow detection of change over time. The pelagic seabird database contains distribution and abundance data on marine birds at-sea and will be managed by the U.S.F.W.S. in Anchorage, Alaska. All databases will be accessible on the internet, and will allow scientists and managers to quickly access information on seabird populations over broad temporal and spatial scales. Used in conjunction with other existing physical and biological data sets, these resources will enhance our understanding about how, when, where, and why seabird populations change over time. Identifying the underlying mechanisms responsible for population variability represents a critical first step, necessary to build predictive habitat use and demographic models required to forecast the fate of seabird populations and species in a dynamic marine environment.

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REFERENCES

AEBISCHER, N.J., COULSON, J.C. & COLEBROOK, J.M. 1990. Parallel long-term trends across four marine trophic levels and weather. *Nature* 347: 753-755.

AINLEY, D.G. 2002. The Ross Sea, Antarctica, where all ecosystem processes still remain for study, but maybe not for long. *Marine Ornithology* 30: 55-62.

ARENDT, A.A., ECHELMEYER, K.A., HARRISON, W.D., LINGLE, C.S. & VALENTINE, V.B. 2002. Rapid wastage of Alaska glaciers and their contribution to rising sea level. *Science* 297: 382-386.

BALLANCE, L.T., PITMAN, R.L. & REILLY, S.B. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* 78:1502-1518.

BLOCK, B.A., COSTA, D.P., BOEHLERT, G.W. & KOCHEVAR, R.E. 2002. Revealing pelagic habitat use: the tagging of Pacific pelagics program. *Oceanologica Acta* 25: 255-266.

BOGRAD, S.J. & LYNN, R.J. 2003. Long-term variability in the Southern California Current System. *Deep-Sea Research II* 50: 2355-237.

BOERSMA, P.D. & PARRISH, J.K. 1999. Limiting abuse: marine protected areas, a limited solution. *Ecological Economics* 31: 287-304.

CROXALL, J.P. 1998. Research and conservation: a future for albatrosses? In: Robertson, G. & Gales, R. (Eds.). Albatross Ecology and Conservation. Chipping Norton: Surrey Beatty and Sons, Ltd. pp. 269-290.

DECKER, C.J. & O'DOR, R. 2002. A census of marine life: unknowable or just unknown? *Oceanologica Acta* 25: 179-186.

FOLLAND, C.K., PARKER, D.E., COLMAN, A.W. & WASHINGTON, R. 1999. Large scale models of ocean surface temperature since the late nineteenth century. In: Navarra, A. (Ed). Beyond El Niño: Decadal and Interdecadal Climate Variability. New York: Springer. pp. 75-102

FURNESS, R.W. & CAMPHUYSEN, C.J. 1997. Seabirds as monitors of the marine environment. *ICES Journal of Marine Science* 54: 726-737

HUNT, G.L., JR., MEHLUM, F., RUSSELL, R.W., IRONS, D.B., DECKER, M.B. & BECKER, P.H. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. *Proceedings of the International Ornithological Congress* 22: 2040-2056.

HUNT, G.L., Jr. & SCHNEIDER, D.C. 1987. Scale dependent processes in the physical and biological environment of seabirds. In: Croxall, J.P. (Ed). Seabirds: their feeding ecology and role in marine ecosystems. Cambridge: Cambridge University Press. pp. 7-41

HYRENBACH, K.D., FORNEY, K.A. & DAYTON, P.K. 2000. Marine Protected Areas and Ocean Basin Management. *Aquatic Conservation: Marine and Freshwater Ecosystems* 10: 437-458.

KITAYSKY, A.S., HUNT, G.L., JR., FLINT, E.N., RUBEGA, M.A. & DECKER, M.B. 2000. Resource allocation in breeding seabirds: responses to fluctuations in their food supply. *Marine Ecology Progress Series* 206: 283-296.

KOOYMAN G.L., ANCEL A. & LE MAHO, Y. 1992. Foraging behavior of Emperor Penguins as resource detector in winter and summer. *Nature* 360: 336-8.

LEVITUS, S., ANTONOV, J.I., BOYER, T.P. & STEPHENS, C. 2000. Warming of the world Ocean. *Science* 287: 2225-2229.

LYVER, P.O., MOLLER, H. & THOMPSON, C. 1999. Changes in Sooty Shearwater *Puffinus griseus* chick production and harvest precede ENSO events. *Marine Ecology Progress Series* 188: 237-248.

MANTUA, N.J., HARE, S.R., ZHANG, Y., WALLACE, J.M. & FRANCIS, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Metereological Society* 78: 1069-1079.

MCGOWAN, J.A. 1990. Climate and change in oceanic ecosystems: the value of time series data. *Trends in Ecology and Evolution* 5: 293-300.

MCGOWAN, J.A., CAYAN, D.R. & DORMAN, L.M. 1998. Climate-ocean variability and ecosystem response in the Northeast Pacific. *Science* 281: 210-217.

MONTEVECCHI, W.A. & MYERS, R.A. 1995. Prey harvest of seabirds reflect pelagic fish and squid abundance on multiple spatial and temporal scales. *Marine Ecology Progress Series* 117: 1-9.

PIATT, J.F., LENSINK, C.J., BUTLER, W., KENDZIOREK, M. & NYSEWANDER, D.R. 1990. Immediate impact of the Exxon Valdez oil spill on marine birds. *Auk* 107: 387-397.

SPEAR, L.B., AINLEY, D.G., NUR, N. & HOWELL, S.N.G. 1995. Population size and factors affecting at-sea distributions of four endangered Procellariids in the tropical Pacific. *Condor* 97: 613-638.

SYDEMAN, W.J., HESTER, M.M., THAYER, J.A., GRESS, F., MARTIN, P. & BUFFA, J. 2001. Climate change, reproductive dynamics, and prey harvest of marine birds in the California Current Marine Ecosystem. *Progress in Oceanography* 49: 309-329.

SYDEMAN, W.J., HYRENBACH, K.D., MORGAN, K.H. & YEN, P.P. 2003. Integration of marine bird and mammal observations with the east-west continuous plankton recorder project. Abstract submitted to the 30th Pacific Seabird Group Annual Meeting, 19-22 February, Parksville, British Columbia.

TASKER M.L., CAMPHUYSEN, C.J., COOPER, J., GARTHE, S., MONTEVECCHI, W.A. & BLABER, S.J.M. 2000. The impacts of fishing on marine birds. *ICES Journal of Marine Science* 57: 531-547.

VEIT, R.R., MCGOWAN, J.A., AINLEY, D.G., WAHL, T.R. & PYLE, P. 1997. Apex marine predator declines ninety percent in association with changing oceanic climate. *Global Change Biology* 3: 23-28.

WEIMERSKIRCH, H., WILSON, R.P., GUINET, C. & KOUDIL, M. 1995. Use of seabirds to monitor sea-surface temperatures and to validate remote-sensing measurements in the Southern Ocean. *Marine Ecology Progress Series* 126: 299-303.

WILSON, R., GREMILLET, D., SYDER, J., KIERSPEL, M.A.M., GARTHE, S., WEIMERSKIRCH, H., SCHAFER-NETH, C., SCOLARO, J.A., BOST, C.A., PLOTZ, J. & NEL, D. 2002. Remote-sensing systems and seabirds: their use, abuse and potential for measuring marine environmental variables. *Marine Ecology Progress Series* 228: 241-261.

WOEHLER, E.J. 1996. Concurrent declines in five species of Southern Ocean seabirds in Prydz Bay. *Polar Biology* 5: 379-382.

WOOLLER, R.D., BRADLEY, J.S. & CROXALL, J.P. 1992. Long-term population studies of seabirds. *Trends in Ecology and Evolution* 7: 111-114.

BIOGEOGRAPHY OF PROCELLARIIFORM FORAGING STRATEGIES: DOES OCEAN PRODUCTIVITY INFLUENCE PROVISIONING?

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SUMMARY

BADUINI, C.L. & HYRENBACH, K.D. 2003. Biogeography of Procellariiform foraging strategies: does ocean productivity influence provisioning? *Marine Ornithology* 31: 101-112.

Mounting evidence suggests that tubenose seabirds (Order Procellariiformes) balance the costs of parental care and the maintenance of adult body condition by regulating the duration of foraging trips during the chick-rearing period. In particular, several species exhibit a bimodal foraging strategy, alternating short (nearshore, 1-5 d) and long (offshore, 6-29 d) foraging trips. We conducted a literature review to assess the biogeographic correlates of provisioning strategies among Procellariiform seabirds, focusing our analysis on the taxonomic affiliation, geographic breeding location (i.e., latitude), and the extent of shallow shelves in the vicinity of breeding colonies. Although our statistical analysis indicated no significant differences in foraging strategies among tubenose families, the bimodal pattern has only been documented in the albatrosses (Diomedeidae) and the shearwaters and petrels (Procellariidae), being absent from the storm petrels (Hydrobatidae) and the diving petrels (Pelecanoididae). We also detected a higher incidence of the bimodal strategy in tropical-subtropical and temperate areas, compared to higher latitude polar-subpolar regions. Considering all the species surveyed, the delivery rates (% BM day^{-1}) were greatest for the shortest foraging trips and decreased with increasing trip length. Among bimodal species, delivery rates were significantly greater for short (mean = 9.8 % BM day^{-1}) than for long foraging trips (mean = 2.6 % BM day^{-1}). However, seabirds increased their effective delivery rates by alternating several short foraging trips for every long excursion. The resulting effective dual prey delivery rates, after combining short and long foraging trips, were undistinguishable from those for species with a unimodal foraging strategy. Additionally, we tested whether the use of a bimodal provisioning strategy was related to the spatial and temporal patterns of ocean productivity. We observed significantly greater chlorophyll a concentrations within the more distant foraging grounds (long trip destinations) targeted by bimodal species. Conversely, we did not detect a difference in the variability of chlorophyll a concentrations within the two types of foraging grounds, suggesting that ocean productivity is equally predictable within the areas targeted by long and short provisioning trips. Our results highlight the importance of ocean productivity patterns as determinants of marine bird foraging strategies and distributions during the breeding season.

Keywords: Provisioning, foraging ranges, bimodal foraging strategy, unimodal foraging strategy, delivery rate, Procellariiform, ocean productivity

INTRODUCTION

Tubenose seabirds (Order Procellariiformes) exhibit exceptional life-history traits with high and extended parental care, while foraging on distant and unpredictable marine resources (Warham 1990, 1996). Procellariiformes may resolve these constraints in three ways. First, parents frequently overfeed their young to buffer them from an excessive body mass loss during periods of sparse prey resources and low provisioning (Lack 1968, Ashmole 1971). Second, tubenose seabirds have developed the ability to deliver energy-rich prey in a processed form, namely stomach oil, allowing them to feed chicks very energy-dense prey after prolonged foraging trips to sea (Place *et al*. 1989, Roby *et al*. 1989). Third, recent evidence suggests that many Procellariiformes, including albatrosses and shearwaters, employ a dual foraging strategy of interspersed long and short foraging trips designed to provide their young while maintaining adult body condition during the chick-rearing period (Weimerskirch *et al*. 1994a, Granadeiro 1998, Weimerskirch & Cherel 1998, Booth *et al*. 2000). Short foraging trips (1-5 days), typically targeting onshore areas in the vicinity of the colony, are energetically beneficial for chicks and costly for adults. Conversely, long foraging trips (6-29 days) to offshore waters help maintain parental body mass but result in lower food delivery rates (g day^{-1}) to the chick. Thus the decision to engage in a short (onshore) or a long (offshore) foraging trip represents a compromise between the energetic requirements of the parents and the chick (Weimerskirch *et al*. 1994a, Weimerskirch & Cherel 1998).

The bimodal foraging strategy was first reported for the blue petrel *Halobaena caerulea*; (Chaurand & Weimerskirch 1994) and subsequently for three other Procellariiform taxa nesting on subantarctic islands, the Thin-billed Prion *Pachyptila belcheri*, the Yellow-nosed Albatross *Diomedea chlororhynchos*, and the Wandering Albatross *Diomedea exulans* (Weimerskirch *et al*. 1994a). Since these initial observations, numerous publications have described similar foraging strategies in other tubenose species from temperate and subpolar regions. However, this strategy is by no means universal in the Procellariiformes. Dual foraging trips are not consistently observed from year to year within a given population, or across allopatric populations of the same species. In addition, the alternating sequence of short/long foraging trips varies greatly within a given species. While some populations switch between one long and one short trip, others alternate one long excursion for every three to six short trips. Moreover, some bimodal species do not regularly alternate between short and long foraging trips, but switch between the two, depending on the body condition of the parent.

Our objective was to explore potential biogeographic correlates of provisioning strategies in Procellariiform seabirds. In particular, we wanted to assess the relationship between a foraging strategy and taxonomy (e.g., family affiliation), breeding location (e.g., colony latitude), habitat (e.g., extent of shelf area surrounding the colony), and ocean productivity (e.g., chlorophyll concentration). To determine if there was a difference in the profitability of the unimodal and the bimodal provisioning patterns across taxa, we compared the absolute (g day^{-1}) and standardized (% body mass day^{-1}) delivery rates for short and long foraging trips of the same species. The average delivery rates (% mass day^{-1}) were also compared, after weighting long and short trips by their relative frequency, for species that exhibit bimodal and unimodal foraging patterns. Lastly, we compared ocean productivity patterns (e.g. the mean and coefficient of variation in chlorophyll a concentration) at those areas visited during long and short foraging trips, to determine if foraging strategies were related to the abundance and the predictability of prey resources.

METHODS

We summarized a collection of 50 published articles, spanning the years 1985-2003, and some unpublished results made available by individual investigators (Table 1). Not all studies aimed to determine whether breeding birds employed a dual strategy of short and long foraging trips. However, if the papers provided detailed information regarding the variability in trip length, we assigned the study population to a bimodal or a unimodal foraging strategy. For a population to be assigned to the former pattern, the histogram of foraging trip durations had to show a distinct bimodal shape. If no distinct bimodality was observed, the population was assigned to a unimodal foraging pattern. Thus, this dichotomy was based solely on the shape of the frequency distribution of foraging trip durations. The absolute length of the foraging trips was not considered.

Before we could assess potential environmental correlates of provisioning patterns in the Procellariiform seabirds, we had to ascertain whether the foraging patterns were related to taxonomic affinity (i.e., family). Once we had discounted potential taxonomic biases, we determined whether the latitude of the breeding locations influenced Procellariiform foraging strategies. We considered four domains on the basis of long-term average sea surface temperature (SST) data from the World Ocean Database 1998 (WOA 1998; http://las.pfeg.noaa.gov): tropical (> 23º C), subtropical (15-23º C), temperate (5-15º C), and polar-subpolar (0-5º C) (Ashmole 1971, Lalli & Parsons 1997). These long-term monthly averages have a spatial resolution of 1 degree latitude/longitude and covered the time period 1945-1996 (Boyer *et al*. 1998). We calculated the mean SST for each study colony by averaging the monthly temperature values for the time period overlapping the satellite telemetry studies (Table 1).

Because the presence of highly-productive continental shelves could also influence the availability of localized prey to breeding seabirds, we tested whether foraging strategies were correlated with the extent of shelf area surrounding breeding colonies. We obtained bathymetric data from NOAA's National Geophysical Data Center ETOPO 5-minute gridded elevation dataset (NGDC 1998) and determined the extent of the contiguous shelf area (depth ≤ 200 m) surrounding each study colony. Because these bathymetric data are relatively coarse (pixel size: 5-10 km), we considered three broad continental shelf categories: small (area < 500 km^2), intermediate (area between 500 and 5000 km^2), and large (area > 5000 km^2) (Table 1). Finally, we assessed if there were differences in the provisioning rates and the ocean productivity patterns (i.e., phytoplankton standing stocks) within the foraging grounds targeted during short and long provisioning trips by those species exhibiting a bimodal strategy.

We determined the foraging grounds for those study populations where published tracking studies had been conducted during the chick-rearing period, or where there was information on the foraging locations of chick-provisioning individuals. Foraging grounds were mapped using four types of data: telemetry information, dietary studies, estimates of the average trip duration and flight speed, and at-sea observations of foraging birds (Table 1). Three types of telemetry data were considered: satellite tracking locations, movement tracks, and kernel activity ranges. For studies that reported raw locations and tracks, we determined those areas where the birds seemed to engage in searching behavior, characterized by contorted paths and slower movement rates. For articles that provided kernel plot estimates, which depict where satellite-tracked individuals spent their time at sea, we selected "core" activity areas delineated by the 50% time contour. In some cases, the satellite tracking was conducted in conjunction with provisioning and dietary studies at breeding colonies. In other instances, the tracking data did not overlap temporally with provisioning and dietary studies at the colonies.

Second, some provisioning papers provided information regarding general foraging areas, based upon the types of prey (e.g., pelagic versus neritic) brought back to the nest after each type of foraging trip (e.g., long versus short). Other studies estimated the maximum roundtrip distance traveled by foraging birds, by dividing the amount of time spent away from the colony (trip duration) by the average flight speed. Finally, at-sea observations of foraging birds during the chick-rearing period also were used to identify the destinations of short and long foraging trips.

Once the foraging grounds targeted by short and long foraging trips were mapped, we quantified the patterns of ocean productivity within these areas using remotely-sensed ocean color imagery. Values of Chlorophyll a concentration (chl a) were derived from level 3 Sea-viewing Wide Field-of-view Sensor (SeaWiFS) monthly composites, with a spatial resolution of 9 km. The Goddard Space Flight Center filters, calibrates, and converts satellite-derived radiometric measurements into estimates of chlorophyll a, the main photosynthetic pigment produced by phytoplankton in the marine environment (Perry 1986, Hooker & McClain 2000), and makes these data available at the SeaWiFS project web-site (http://seawifs.gsfc.nasa.gov/SEAWIFS.html). Satellite estimates are within 35% of concurrent in-situ observations within the range of chlorophyll a concentration between 0.05-50 mg m^{-3} (Hooker & McClain 2000). The biggest discrepancies between in-situ and satellite measurements occur in areas of high chlorophyll a concentrations, ranging between 1-10 mg m^{-3} (Kahru & Mitchell 1999).

To ensure that the dietary and foraging range data were representative of the published foraging destinations and

TABLE 1
Biogeography of provisioning patterns of (A) Northern and (B) Southern Hemisphere Procellariiform seabirds.

(A) Species	Breeding Location	Foraging Strategy	Short Trips (d)	Long Trips (d)	Shelf Habitat	Mean Monthly SST	Body Size (kg)	Study Dates	Reference
DIOMEDEIDAE									
Laysan Albatross (*Phoebastria immutabilis*)	Tern Island, French Frigate Shoals, Hawaii	B_{na}	1-6	12-28	SS	24.32	3	Jan-Jun 98-99 Jan-Jun 98-99	Fernández *et al*. 2001 Hyrenbach *et al*. 2002
Black-footed Albatross (*Phoebastria nigripes*)	Tern Island, French Frigate Shoals, Hawaii	B_{na}	1-4	12-29	SS	24.32	3.2	Jan-Jun 98-99 Jan-Jun 98	Fernández *et al*. 2001 Hyrenbach *et al*. 2002
PROCELLARIIDAE									
Cory's Shearwater (*Calonectris diomedea*)	Svelagem Grande, NE Atlantic	B	1-2	3-9*	SS	22.34	0.89	Aug-Sep 97	Granadeiro *et al*. 1998
Cory's Shearwater (*Calonectris diomedea*)	Berlenga, Portugal	U	1-3		LS	18.77	0.89	Aug-Sep 96	Granadeiro *et al*. 1998
Wedge-tailed Shearwater (*Puffinus pacificus*)	Tern Island, French Frigate Shoals, Hawaii	U	1-2		SS	26.74	0.40	Aug-Oct 96 Sep-Nov 97	Baduini 2002
Manx Shearwater (*Puffinus puffinus*)	Skomer Island, Whales	U / B**	1-4	5-7**	LS	14.22	0.44	May-Aug 99 Jul-Sep 95-96	Gray & Hamer 2001 Hamer *et al*. 1999
Little Shearwater (*Puffinus assimilis*)	Svelagem Grande, NE Atlantic	U	1-2		SS	18.55	0.17	Mar-Apr 93	Hamer 1994
Northern Fulmar (*Fulmarus glacialis*)	Shetland, UK St. Kilda, Scotland	U U	1 1		LS	12.24	0.79	Jul-Sep 97 Jul 94	Phillips & Hamer 2000 Hamer & Thompson 1997
Northern Fulmar (*Fulmarus glacialis*)	Bjornoya, Barents Sea	U	0.3-3.5		LS	5.29	0.85	Jun-Jul 99	Weimerskirch *et al*. 2001
HYDROBATIDAE									
Leach's Storm-petrel (*Oceanodroma leucorhoa*)	Kent Island, New Brunswick	U	1-4		LS	11.62	0.045	Aug 83 Aug 86	Ricklefs *et al*. 1985 Ricklefs 1992
European Storm-petrel (*Hydrobates pelagicus*)	Shetland, UK	U	1-2		LS	10.64	0.029	May-Oct 92 Jul-Nov 93	Bolton 1995a Bolton 1995b

B = Bimodal provisioning strategy; B_{na} = Bimodal trips but no regular alternation between the long and short trips
U = Unimodal provisioning strategy; *Bimodal trips conducted during food limited year only; **Females only conduct bimodal provisioning pattern; ***Parents coordinate bimodal forage patterns
Three shelf habitats are considered: SS = Small shelf (< 500 km^2); LS = Large Shelf (> 5000 km^2); IS = Intermediate Shelf (500-5000 km^2)

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TABLE 1
Biogeography of provisioning patterns of (A) Northern and (B) Southern Hemisphere Procellariiform seabirds.

(B) Species	Breeding Location	Foraging Strategy	Short Trips (d)	Long Trips (d)	Shelf Habitat	Mean Monthly SST	Body Size (kg)	Study Dates	Reference
Diomedeidae									
Black-browed Albatross (*Diomedea melanophris*)	Kerguelen Island	U	1-9		IS	5.19	3.7	Dec-Jan 91-92 Feb 94-95	Weimerskirch *et al*. 1994a Weimerskirch *et al*. 1997a
Black-browed Albatross (*Diomedea melanophris*)	Bird Island, South Georgia	U	1-12		IS	2.79	3.7	Jan-Jun 90 Jan-Jun 92-94	Huin *et al*. 2000
Grey-headed Albatross (*Diomedea chrysostoma*)	Bird Island, South Georgia	U	1-12		IS	2.79	3.4	Jan-Jun 93-96	Huin *et al*. 2000
Shy Albatross (*Thalassarche cauta*)	Albatross Island, Tasmania	U	1-2		LS	16.13	4.5	Jan-Feb 96 Jan-Feb 97	Hedd *et al*. 2001 Hedd *et al*. 2002
Wandering Albatross (*Diomedea exulans*)	Possession Island, Crozet	B	1-5	6-20	SS	5.68	9.3	Dec-Jan 91-92 Jun-Jul 92	Weimerskirch *et al*. 1994b Weimerskirch *et al*. 1997b
Wandering Albatross (*Diomedea exulans*)	Bird Island, South Georgia	B	1.5-3	12-18	IS	1.74	10	May-Aug 96-97	Berrow *et al*. 2000
Waved Albatross (*Phoebastria irrorata*)	Isla Española, Galapagos Islands	B	1-5	>7	IS	21.04	4.5	Jun-Oct 96	Fernández *et al*. 2000
Yellow-nosed Albatross (*Diomedea chlororhynchos*)	Amsterdam Island	B	1-5	6-12	IS	15.41	2.1	May-Aug 90 Dec-Mar 95-96	Weimerskirch *et al*. 1994a Weimerskirch *et al*. 2000a
Procellariidae									
Antarctic Petrel (*Thalassoica antarctica*)	Svarthamaren, Antarctica	U	3-9		LS	1.05	0.69	Dec-Feb 91-92 Dec 96-Feb 97	Lorentsen *et al*. 1996 Tverra *et al*. 1998
Blue Petrel (*Halobaena caerulea*)	Kerguelen Island	B	1-3	5-10	IS	5.19	0.17	Jan-Feb 90	Chaurand & Weimerskirch 1994
Little Shearwater (*Puffinus assimilis*)	Lady Alice Island, New Zealand	B	1-2	7***	LS	15.88	0.22	Aug-Dec 94	Booth *et al*. 2000
Sooty shearwater (*Puffinus griseus*)	Snares Island, New Zealand	B	1-2	8-17	LS	12.25	0.85	Feb-Mar 95	Weimerskirch 1998
Short-tailed Shearwater (*Puffinus tenuirostris*)	Bruny Island, Tasmania	B	1-3	9-17	LS	15.05	0.70	Jan 97 Mar 97	Weimerskirch & Cherel 1998
Thin-billed Prion (*Pachyptila belcheri*)	Kerguelen Island	B	1-3	5-9	IS	5.19	0.13	Dec-Jan 91-92	Weimerskirch *et al*. 1994a
Wedge-tailed Shearwater (*Puffinus pacificus*)	Heron Island, Great Barrier Reef Australia	B	1-3	8	LS	26.28	0.38	Feb-Mar 01-02	B. Smithers (unpubl. data)
White-chinned Petrel (*Procellaria aequinoctialis*)	Possession Island, Crozet	B	0.5-2	3-13	SS	5.98	1.5	Jan-Feb 97	Catard *et al*. 2000
Pelecanoididae									
Common Diving Petrel (*Pelecanoides urinatrix*)	Kerguelen Island Bird Island, South Georgia	U	1-3		IS	5.19 3.31	0.15	Dec-Jan 91-92 Jan-Feb 1982	Weimerskirch *et al*. 1994a Roby 1991

provisioning rates, we restricted our analyses to those months where there was concurrent information about foraging ranges and provisioning rates. SeaWiFS imagery was obtained for those chick-rearing months that overlapped the tracking/provisioning studies of each study population (Table 2), and these data were used to calculate the average and the variability in ocean productivity within different foraging areas. We discarded unreasonably high chlorophyll a concentrations (≥ 50 mg m^{-3}) resulting from high cloud cover reflectance (Hooker & McClain 2000), and calculated the median for the remaining pixels within each foraging area. We repeated this procedure for every month each population was studied, using the five years of SeaWiFS data currently available (January 1998-December 2002).

To assess the climatology of ocean productivity patterns within the foraging grounds exploited by chick-provisioning seabirds, we averaged the monthly medians across years (1998-2002). In addition to calculating this long-term average, the annual values were used to determine the temporal variability in ocean productivity, using the coefficient of variation [CV = (standard deviation/mean) * 100%] across all months and years. The coefficient of variation provides a standardized measure of variability, scaled by the magnitude of the mean (Zar 1984).

We quantified the spatial and temporal variability in ocean productivity patterns in two ways. First, to determine if there were significant differences in ocean productivity within the foraging grounds targeted by short and long provisioning trips, we compared the mean chlorophyll a concentrations for species with a bimodal foraging strategy. Then, we contrasted the variability (CV) of these pigment values to determine if ocean productivity was more predictable within the foraging grounds far/close to breeding colonies. More specifically, we used paired t-tests to contrast the chlorophyll a concentrations for the long and the short foraging destinations on a species-specific basis. Thus, the sample size of each test was eight paired species-specific measurements (Table 2).

Finally, to explore whether a unimodal foraging strategy (e.g., exploiting nearby resources) could be as profitable as a bimodal mode (e.g., alternating between near and distant prey), we compared species-specific delivery rates (g day^{-1}) for both types of foraging trips. Although delivery rates were not recorded in every study, they could be estimated using the ratio of the average meal size and the average trip duration for short and long foraging excursions separately. To compare among taxa of varying body size, delivery rates were normalized as the percentage of the adult body mass delivered to the chick per day (% BM day^{-1}). Adult body mass information, was usually provided within the provisioning results. However, when unavailable, other published sources were used to obtain information on average adult body mass for the specific population and colony where the provisioning study was conducted. Paired t-tests were used to determine if delivery rates were significantly different for short and long trips by a given population. Additionally, the delivery rates for species that conduct several short trips for every long foraging excursion were weighted using the ratio of short to long trips conducted. The effective bimodal delivery rates resulting from combining short and long trips were then compared to those for unimodal species. Since delivery rates were expressed as a percentage of adult body mass and percentage data are typically non-normally distributed, all delivery rate values were arc sine transformed before performing the statistical analyses (Zar 1984).

RESULTS

We observed a great variety of foraging strategies in Procellariiform seabirds, ranging from unimodal foraging trips, to the alternation of 1-6 short foraging trips for every long excursion We summarized 12 unimodal and 14 bimodal Procellariiform species (Table 1). The species that exhibited a bimodal foraging strategy alternated between short trips to nearshore feeding grounds along continental shelves adjacent to breeding colonies, and long trips to pelagic waters associated with polar and sub-polar frontal zones (Fig. 1, Table 2). Short trips ranged from 1-3 d duration in the medium-sized shearwaters to 1-9 d in the larger albatrosses (Table 1). Long trips ranged from 5-17 days across all albatross and shearwater populations studied. However, not all species regularly alternated between short and long forays, with substantial interspecific variability in the ratio of short/long foraging trips. In shearwaters, two short feeding excursions were conducted for every long foraging trip (Granadeiro *et al*. 1998, Weimerskirch & Cherel 1998, Weimerskirch 1998), except for the Little Shearwater (*Puffinus assimilis*) which exhibited a 6/1 ratio (Booth *et al*. 2000). In the Wandering Albatross, five short trips were undertaken for every long excursion (Berrow *et al*. 2000).

Our study revealed a significant association between Procellariiform foraging strategies and ocean productivity patterns, once we had accounted for taxonomic and geographic biases. There was no significant association between taxonomic affiliation (i.e., family) and foraging pattern (i.e., unimodal or bimodal) (Table 1; Chi-Square Log likelihood ratio = 5.84, $P = 0.120$, df = 3, n = 28). This result suggests that the taxonomic affiliation of a species does not determine the adoption of a unimodal or bimodal foraging strategy in Procellariiform seabirds. However, it is worth noting that bimodal species are disproportionately represented in the albatrosses (Diomedeidae) and the shearwaters and petrels

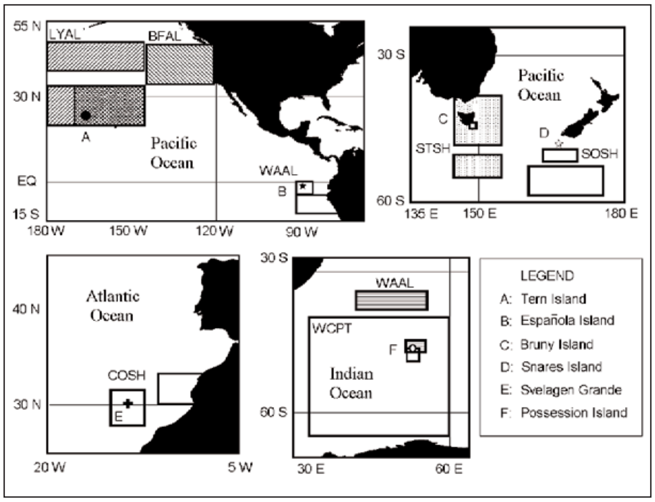

Fig. 1. Breeding locations and foraging ranges of the eight bimodal species listed in Table 2. The Black-footed Albatross (BFAL) and Laysan Albatross (LYAL) at Tern Island, Hawaii (black circle, A), the Waved Albatross (WAAL) at Española Island, Galapagos (black star, B), the Short-tailed Shearwater (STSH) at Bruny Island, Tasmania (white square, C), the Sooty Shearwater (SOSH) at Snares Island, New Zealand (white star, D), the Cory's Shearwater (COSH) at Svelagem Grande, (black cross, E), and the White-chinned Petrel (WCPT) and the Wandering Albatross (WAAL) at Possession Island, Crozet (white circle, F).

TABLE 2

Mean and variability (CV) in chlorophyll a concentration (mg m^{-3}) of cell grids (9 X 9 km) within Procellariiform foraging ranges targeted by short (ST) and long (LT) foraging trips. Four methods were used to delineate the foraging grounds: foraging range (trip duration divided by average flight speed, FR) estimates; locations (TL), tracks (TT) and kernel plots of satellite tracking data (KP); at-sea observations (OB); and diet during foraging trips (DI).

Species	Location	ST Range	LT Range	Mean chl a ST	CV chl a ST	Mean chl a LT	CV chl a LT	Method of determination (Reference)
UNIMODAL								
Cory's Shearwater (*Calonectris diomedea*)	Berlenga, Portugal	38-41 N 8-11 W	-	0.283	27.01	-	-	FR, OB (Granadeiro *et al*. 1998)
Black-browed Albatross (*Diomedea melanophris*)	Kerguelen Islands	47-50 S 69-71 E	-	0.826	26.70	-	-	TL (Weimerskirch *et al*. 1997a)
Shy Albatross (*Thalassarche cauta*)	Albatross Island, Tasmania	40-42 S 143.5 -145.5 E	-	0.496	19.60	-	-	KP (Hedd *et al*. 2001)
BIMODAL								
Laysan Albatross (*Phoebastria immutabilis*)	Tern Island, Hawaii	20-34 N 145-180 W	38-50 N 145-180 W	0.086	21.43	0.357	12.71	KP (Hyrenbach *et al*. 2002)
Black-footed Albatross (*Phoebastria nigripes*)	Tern Island, Hawaii	20-34 N 145-170 W	34-48 N 121-145 W	0.087	21.29	0.298	19.96	KP (Hyrenbach *et al*. 2002)
Cory's Shearwater (*Calonectris diomedea*)	Svelagem Grande, NE Atlantic	28-31 N 14-17 W	30-33 N 9-12 W	0.107	13.84	0.184	20.62	FR (Granadeiro *et al*. 1998)
Waved Albatross (*Phoebastria irrorata*)	Isla Española, Galapagos Islands	0-4 S 86-93 W	4-10 S 78-86 W	0.418	34.78	0.556	21.81	TL (Fermández *et al*. 2001)
Wandering Albatross (*Diomedea exulans*)	Possession Island, Crozet	46-47 S 51-53 E	34-38 S 40-55 E	0.162	12.64	0.253	17.28	KP (Weimerskirch *et al*. 1997b)
Short-tailed Shearwater (*Puffinus tenuirostris*)	Bruny Island, Tasmania	38-48 S 145-155 E	50-55 S 145-155 E	0.263	16.60	0.219	10.16	TL, DI, OB (Weimerskirch & Cherel 1998)
Sooty shearwater (*Puffinus griseus*)	Snares Island, New Zealand	48-51 S 163-170 E	52-58 S 160-176 E	0.238	17.76	0.337	16.32	(Weimerskirch 1998)
White-Chinned Petrel (*Procellaria aequinoctialis*)	Possession Island, Crozet	46.5-47 S 51-52 E	40-65 S 30-60 E	0.288	33.51	0.227	16.40	TT (Catard *et al*. 2000)

(Procellariidae), while no storm-petrels (Hydrobatidae) and diving petrels (Pelecanoididae) have been documented to employ a dual foraging mode.

Moreover, bimodal species appear to be concentrated south of the equator. In the northern hemisphere, two species of albatross and three shearwaters employed a bimodal foraging pattern. However, although Laysan *Phoebastria immutabilis* and Black-footed Albatrosses *P. nigripes* undertake long and short foraging trips during the chick-rearing period, there is no evidence of a progressive alternation between long and short trips. Interestingly, no Northern Fulmar *Fulmarus glacialis* population has been documented to employ a dual foraging strategy, in spite of the broad range of this species. In the southern hemisphere, the dual foraging pattern is pervasive, and has been observed in three of six albatross species previously studied, the Yellow-nosed *Diomedia chlororhynchos*, the Wandering *D. exulans*, and the Waved *P. irrorata* Albatross. Additionally, six petrel species, including four shearwaters, the Blue Petrel, and the Thin-billed Prion conduct bimodal foraging trips, and there is evidence that in at least another species, the Little Shearwater, there is alternation and coordination of short and long foraging trips among parents (Booth *et al*. 2000, Smithers unpubl. data).

The analysis of Procellariiform provisioning strategies with respect to the geographic location of breeding colonies revealed no significant difference in the distribution of populations exhibiting a bimodal foraging strategy across tropical-subtropical (0-35º N and S), temperate (35-50º N and S), and polar subpolar (> 50º N and S) regions (Chi-Square Log likelihood ratio = 5.37, P = 0.068, df = 2, n = 28). Only one of the five (20%) polar-subpolar populations considered in this analysis exhibited a bimodal foraging pattern, while 71% and 67% of the populations breeding in tropical-subtropical and temperate latitudes employed this strategy respectively.

There were no significant relationships between the size of shelf area surrounding colonies and foraging strategy (Chi-Square Log likelihood ratio = 2.11, P = 0.348, df = 2, n = 28). A greater percentage (71% and 67% respectively) of the species breeding in colonies surrounded by small and intermediate shelf areas used a bimodal foraging strategy, relative to the species breeding in areas characterized by large (area > 5000 km^2) continental shelves (42% bimodal species).

We detected significantly greater mean chlorophyll a concentrations within the foraging areas targeted by Procellariiform seabirds during long (mean = 0.30 +/- 0.04 SE mg m^{-3}) than in areas of short foraging trips (mean = 0.21 ± 0.04 SE mg m^{-3}) (Table 2; Paired t-test among individual species $t_{\text{two-tailed}}$ = -2.45, P = 0.045, df = 7, n = 8). This result suggests that the foraging grounds where petrels go to feed on long forays are relatively more productive than those areas where they fed during short foraging trips. However, there was no significant difference in the variability in chlorophyll a (CV) within the areas where Procellariiform seabirds feed during long (mean = 16.91 ± 1.41 SE) and short (mean = 21.48 ± 2.97 SE) foraging trips (Paired $t_{\text{two-tailed}}$ = 1.56, P = 0.163, df = 7, n = 8).

For species in which both unimodal and bimodal strategists have been observed, the delivery rate of food (% BM day^{-1}) was greatest for the foraging trips of the shortest duration, and decreased with increasing trip length (Grandeiro *et al*. 1998, Baduini 2002). Overall, among those species that conducted a bimodal foraging strategy, the delivery rates were significantly greater (Paired $t_{\text{two-tailed}}$ = 9.82, P < 0.001, n = 10) for short (mean = 9.83 ± 1.35 SE% BM day^{-1}) than for long (mean = 2.50 ± 0.39% BM day^{-1}) foraging trips (Table 3). Furthermore, bimodal species increased their effective provisioning rates by conducting several short foraging trips for every long excursion.

Once we adjusted the delivery rates of bimodal species to account for the unequal sequence of short and long foraging trips, we detected no significant difference (t = -1.93, $P_{\text{two-tailed}}$ = 0.069, n = 20) in the delivery rates (% BM day^{-1}) of unimodal species (mean = 9.39 +/- 0.97 SE) compared with the effective provisioning rates of bimodal species with a mixed foraging strategy (mean = 6.97 ± 0.79 SE). In fact, there was no significant difference (t = 0.17, $P_{\text{two-tailed}}$ = 0.870, n = 20) between the delivery rates of unimodal species and those for bimodal taxa engaged exclusively in short trips (Table 3).

DISCUSSION

This review addresses the taxonomic and geographic determinants of foraging strategies in Procellariiform seabirds at a broad, multi-species level. Since the discovery of a novel dual provisioning strategy in Southern Ocean Procellariiform seabirds (Chaurand & Weimerskirch 1994, Weimerskirch *et al*. 1994), the use of bimodal foraging trips has been increasingly reported for other tubenose species around the world. Nevertheless, this dual strategy is not ubiquitous across all Procellariiform taxa. In those species with bimodal trip distributions, there appears to be some plasticity in this foraging behavior with gender-based differences, disparities across colonies, and substantial year-to-year variability (Granadeiro *et al*. 1998, Hamer *et al*. 1999, Gray & Hamer 2001). Substantial within-population variability has been documented across genders, as well as from year to year. For example, there is evidence of significant differences among genders, as in the Manx Shearwater *Puffinus puffinus*, where only females engaged in a bimodal foraging pattern. Males, on the other hand, conducted 1-4 day-long unimodal foraging trips and delivered food at a greater rate, thus making a greater overall contribution to chick provisioning than females (Hamer *et al*. 1999, Gray & Hamer 2001). Additionally, researchers have documented interannual variability. Cory's Shearwaters (*Calonectris diomedea*), for instance, employed a flexible foraging strategy with relatively uniform feeding intervals during years of "average" food availability, and a dual foraging strategy (long and short trips) in "low" food years (Granadeiro *et al*. 1998).

Despite this great deal of variability, several results emerged across the studies we reviewed. One pervasive pattern we observed was the negative relationship between provisioning rate and foraging trip duration. Although the meals delivered to the young tended to be larger after longer foraging trips, the average amount of food provisioned per day decreased with increasing trip length. It is interesting that the effective prey delivery rates of the dual strategy (% BM day^{-1} for short and long trips combined) were just as profitable as those for the species with a unimodal foraging trip distribution. Moreover, the delivery rates for short trips in bimodal species were indistinguishable from those of taxa with a unimodal foraging strategy. Thus, the question remains, what is the function of the long foraging trips if chick-provisioning rates for bimodal/unimodal foraging strategies are the same?

TABLE 3

Prey delivery rates (g day^{-1} and % BM day^{-1}) for species that exhibit unimodal and bimodal provisioning patterns. ST = Short foraging trips. LT = Long foraging trips.

Species	Body Mass (kg)	Delivery rate (g/day)		Delivery rate (% BM/day)		Ratio ST/LT	Average delivery rate (ST / LT) combined
		ST	LT	ST	LT		
Unimodal							
Black-browed Albatross	3.7	266	-	7.1	-	-	7.1
Grey-headed Albatross	3.4	253	-	7.5	-	-	7.5
Shy Albatross	4.5	400	-	8.9	-	-	8.9
Antarctic Petrel	0.69	38	-	5.5	-	-	5.5
Cory's Shearwater	0.89	48	-	5.4	-	-	5.4
Little Shearwater	0.17	22	-	13.0	-	-	13.0
Northern Fulmar	0.80	75	-	9.3	-	-	9.3
Wedge-tailed Shearwater	0.40	45	-	11.4	-	-	11.4
European Storm-petrel	0.029	3	-	11.4	-	-	11.4
Leach's Storm-petrel	0.045	4	-	8.0	-	-	8.0
Common Diving Petrel	0.15	23	-	15.8	-	-	15.8
Bimodal							
Wandering Albatross	9.3	341	98	3.7	1.1	5/1	3.3
Yellow-nosed Albatross	2.1	142	53	6.7	2.5	ND	4.6**
Blue Petrel	0.17	30	9	17.5	5.3	1/1	11.4
Cory's Shearwater	0.89	45	20	5.1	2.4	2/1	4.2
Little Shearwater	0.22	21	3	9.6	1.6	6/1	8.5***
Manx Shearwater	0.44	53	10*	12.1	2.3	ND	7.2**
Short-tailed Shearwater	0.70	60	14	8.6	2.1	2/1	6.4
Sooty Shearwater	0.85	96	18	11.2	2.1	2/1	8.2
Thin-billed Prion	0.13	20	5	14.9	3.9	ND	9.4**
White-chinned Petrel	1.5	133	26	8.9	1.7	2/1	6.5

* Females only conduct bimodal foraging trips
** Assuming a ST/LT ratio of 1:1
*** Parents coordinate bimodal foraging trips

ND = no data available

A likely function of long foraging trips may be to restore the body condition of breeding adults, by increasing their own rate of resource provisioning at the expense of a lower feeding rate for the offspring. According to this scenario, the trade-off between self-maintenance and the delivery of resources to the chick influences the ratio of long and short foraging trips. Empirical evidence suggests that the body condition of the adults determines whether they engage in a short or a long foraging trip. Sooty and Short-tailed Shearwaters, for instance, conduct several consecutive short foraging trips (usually two) until the parent body condition reaches a threshold level, and subsequently make a long foraging trip (Chaurand & Weimerskirch 1994, Weimerskirch & Cherel 1998, Weimerskirch 1998). Decisions about whether to forage near or far from the breeding colonies are thus influenced by parent body condition just prior to leaving the colony, rather than by the condition of the chick. Good parental body condition has been associated with high prolactin blood levels and offshore foraging, while poor parental condition has been linked with the onset of long foraging excursions (Weimerskirch & Cherel 1998). Incidentally, adults return to the nest in better body condition after long excursions (e.g., large mass gain), than after short foraging trips (e.g., mass loss) (Weimerskirch *et al.* 1997b).

Conversely, the association between body condition and trip duration does not hold for populations exhibiting a unimodal foraging strategy. For instance, the parental body mass and condition of Wedge-tailed Shearwaters *Puffinus pacificus* nesting in French Frigate Shoals, Hawaii, do not change significantly over the chick-rearing period, and are insensitive to foraging trip duration (Baduini 2002). These results reinforce the notion that long foraging excursions serve to restore adult body mass, and are not required in populations where the condition of breeding birds is not compromised during the chick-rearing period. Moreover, these observations suggest that in those populations and species that employ a bimodal foraging strategy, parental body condition is likely compromised during chick-rearing.

Energetic foraging costs for long and short foraging trips must be considered when a dual foraging strategy is adopted. Energy expended may be 1.5-2.2 times greater for short trips compared to long excursions, as demonstrated in the Blue Petrel (Weimerskirch *et al.* 2003). Thus, the function of longer trips may be to maximize the energetic efficiency of foraging while adults restore their body condition, resulting in lower energetic foraging costs compared to shorter trips. Also, the use of wind for dynamic soaring on long trips has been shown to maximize efficiency by lowering the cost of flight. For instance, in the Wandering Albatross, energetic foraging costs are not correlated to the distance traveled or to flight speed, but are closely related to the number of landings at sea (Weimerskirch *et al*. 2000b, Shaffer *et al*. 2001). Thus, foraging on distant, yet abundant prey resources is likely energetically more efficient than exploiting small unpredictable patches closer to the breeding colony.

Previous provisioning studies have suggested that tubenose species with a bimodal provisioning strategy switch between short trips to less productive waters around colonies, and long foraging excursions to more productive distant areas, frequently associated with subpolar frontal zones (Weimerskirch & Cherel 1998, Weimerskirch 1998). One of the objectives of this study was to test the hypothesis that the purpose of long foraging trips is to target more productive foraging grounds. Additionally, it could be argued that to maintain high chick-provisioning rates during short trips, the foraging grounds close to breeding colonies may represent more predictable foraging grounds, capable of ensuring persistent food resources despite their lower relative ocean productivity. We addressed these hypotheses by comparing the mean and the CV of the chlorophyll a concentration, a metric of ocean productivity, for the destinations of short and long foraging trips undertaken by bimodal species. This paired analysis, involving eight different species addressed by published provisioning papers, revealed that ocean productivity was greater in areas targeted by long foraging trips. On the other hand, the mean chlorophyll a concentrations were equally variable within the foraging grounds close and far from the breeding colonies, suggesting that ocean productivity within the foraging areas targeted by short and long foraging trips are equally predictable.

Because a bimodal foraging strategy could arise in response to several distinct productivity patterns, we propose three possible models for consideration by future provisioning studies: (1) spatially/temporally unpredictable ocean productivity, (2) spatially predictable/temporally shifting ocean productivity, and (3) reliance on diverse resources found exclusively within foraging grounds close and far from breeding colonies. These simplified models are based on the underlying assumption that spatially/temporally predictable and persistent ocean productivity patterns would favor a unimodal foraging pattern, whereby birds commute to the same foraging grounds throughout the provisioning period. Moreover, these models focus exclusively on the spatial and temporal distribution of ocean productivity, and do not incorporate important ecological factors such as interspecific competition, the potential depletion of prey resources in the vicinity of the colony during the breeding season, and the significance of wind patterns for the large-scale movements of foraging birds (e.g., Weimerskirch *et al*. 1985, 1988, 2000b). These factors have been previously invoked to explain the segregation of breeding seabirds, but are beyond the scope of this review.

The spatially/temporally unpredictable ocean productivity hypothesis envisions a scenario whereby, seabirds exploit foraging areas close to and far from breeding colonies to account for temporally and spatially unpredictable ocean productivity. Foragers search for prey as they transit away from the colony towards distant foraging grounds. If the birds encounter sufficient prey within the closer feeding areas, such that prey delivery rates and body condition are maintained, they engage in a short foraging trip. Otherwise, they continue their excursion and venture to distant foraging grounds. This scenario predicts significant differences in ocean productivity across foraging areas (space) or months (time), with the alternation between exploratory searches to foraging grounds in the vicinity of breeding colonies and long foraging trips to distant foraging locations. This model seems particularly appealing for the Wandering Albatross, a species which forages on widely dispersed prey patches not associated with bathymetric habitats and engages in large-scale Levy flight searching patterns suggestive of scale-invariant distribution of prey resources (Weimerskirch *et al*. 1994b, Viswanathan *et al*. 1996).

According to the shifting productivity model, we would expect a significant interaction between chlorophyll a concentrations across months and foraging areas, such that birds engage in short and long foraging trips sequentially to exploit prey resources driven by out-of-phase ocean productivity patterns close and far from their colony. Under this scenario, birds that initially exploit resources in one area, shift to use other foraging grounds as the provisioning season proceeds. These spatio-temporal shifts could be associated with the delayed onset of seasonal (i.e., spring-time) peak in ocean productivity within distant high latitude foraging grounds, and could be influenced by the seasonal migration of frontal zones characterized by high chlorophyll concentrations (e.g., Vinogradov *et al*. 1997, Polovina *et al*. 2001). It is unlikely that this model can be applied to many of the groups reviewed in this paper, because most species regularly alternate between short and long foraging trips throughout the chick-rearing period. However, some Procellariiformes have been observed to increase their foraging ranges and trip lengths as the chick-rearing period progresses (Fernández *et al*. 2001).

The reliance on diverse resources model entails seabirds that are forced to forage within both close and distant localities because they require resources (e.g., specific types of prey, high provisioning rates versus large amounts of food) from each of these foraging grounds. This scenario is difficult to evaluate because the spatial and temporal use of the close/distant foraging grounds would be independent from the underlying ocean productivity patterns. Instead, we predict that the specific requirements of the chick/adult would determine the destination/duration of foraging trips. Thus, studies that address foraging strategies in the context of the diet and the body condition of adults and chicks are required to test this model (Weimerskirch *et al*. 1997b, Weimerskirch 1998, Weimerskirch & Cherel 1998).

Our analysis of ocean productivity patterns within the foraging grounds of Procellariiform seabirds must be interpreted with caution, because it relies on satellite-derived ocean color measurements constrained by two main limitations. Chlorophyll a concentrations (mg m^{-3}) provide a relative measure of the phytoplankton standing stock within an upper layer of the ocean, whose variable depth is determined by the attenuation of light in the water column. Thus, empirical correlations between near-surface and integrated water-column chlorophyll concentrations are required to estimate overall chlorophyll concentrations. Additionally, because the ratio of photo-pigments to carbon in phytoplankton cells is influenced by many factors including species-specific differences, light conditions, and nutrient availability, it is difficult to extrapolate phytoplankton biomass (grams of Carbon) from chlorophyll a concentrations (Gordon & Morel 1983, Perry 1986).

Despite these constraints, remotely-sensed ocean color provides information on relative phytoplankton concentrations, which are useful to characterize spatial and temporal patterns of ocean productivity. In particular, while chlorophyll a concentrations cannot always be directly linked with the rates of carbon fixation by primary producers, this metric does provide a relative index of the amount of phytoplankton available for carrying out primary production and for grazing by zooplankton (Perry 1986, Joint & Groom 2002). In this study, we used the remote sensing ocean color data to obtain a relative index of the spatial and temporal variability in ocean productivity patterns (e.g., Vinogradov *et al.* 1997, Chavez *et al.* 1999). The underlying assumption of our analysis is that ocean productivity influences prey availability to foraging seabirds.

Procellariiform seabirds do not eat phytoplankton, but consume higher trophic-level prey such as zooplankton, fish, and squid (Harper *et al.* 1985). Nevertheless, chlorophyll a concentrations provide valuable information about the physical processes underlying the dispersion of seabird prey over coarse - mega (10s-1000s km) spatial scales (Hunt & Schneider 1987, Hunt *et al.* 1999). In particular, the shallow continental shelves and hydrographic fronts where seabird prey aggregates are characterized by elevated chlorophyll concentrations (Springer *et al.* 1996, Vinogradov *et al.* 1997, Polovina *et al.* 2001). Thus, it is our contention that ocean color imagery can be used to assess the relative productivity of seabird foraging grounds across time (e.g., months and years), and space (e.g., short versus long trip destinations).

In addition to overall ocean productivity, other factors such as the availability (e.g., vertical distribution), the patchiness (i.e., predictability), and the quality (i.e., energy content) of the different prey types available, likely influence whether seabirds engage in a unimodal or a bimodal foraging strategy. Although no studies have quantitatively assessed prey quality for short and long foraging trips, mounting evidence suggests that tubenoses feed their offspring neritic species taken from shelf areas (e.g., euphausiids, fish, squid) after short foraging trips. Conversely, after long foraging trips parents deliver processed prey stored as stomach oil, and offshore fish and squid taken from pelagic waters (Chaurand & Weimerskirch 1994, Weimerskirch *et al.* 1994a, Weimerskirch & Cherel 1998, Catard *et al.* 2000, Cherel *et al.* 2002).

It is essential that researchers undertake studies of the diet and provisioning patterns of satellite-tracked seabirds, within the context of ocean productivity patterns and prey dispersion at sea. Because Procellariiform seabirds engage in extremely long foraging trips, reliance on remote sensing imagery is a necessity to obtain data at the appropriate temporal and spatial scales. Yet, while satellite-derived products provide a fine-scale temporal/spatial resolution of the dynamic ocean processes influencing ocean productivity patterns and prey distributions (Joint & Groom 2000, Nel *et al.* 2001, Hyrenbach *et al.* 2002), an understanding of seabird diet is essential to evaluate different foraging strategies. In particular, by matching the food items delivered to the colony with the oceanographic habitats sampled by foraging seabirds during individual trips, investigators can assess the importance of specific foraging grounds and oceanographic features to provisioning seabirds.

One of the main objectives of this review was to understand the biogeographic determinants of Procellariiform provisioning patterns, to predict whether a specific petrel population should undergo a unimodal or bimodal foraging strategy. It is mostly the larger petrel species (e.g., albatrosses and shearwaters) that employ a dual foraging strategy. Despite some exceptions, the bimodal foraging strategy is prevalent in subantarctic species that breed on offshore islands and alternate foraging trips to the surrounding broad shelf areas with long excursions to subpolar (e.g., Sooty and Short-tailed Shearwater) or subtropical (e.g., Wandering and Yellow-nosed Albatross) frontal zones. While it is conceivable that some of the smaller petrels (e.g., Blue Petrel and Thin-billed Prion) exhibit this same strategy but on smaller temporal scales, no bimodality has been observed in Storm-petrels and Diving petrels.

It is important to note, however, that provisioning studies may have failed to document the dual foraging strategy in species that engage in bimodal foraging trips exclusively during years of "poor" prey availability. Because many provisioning studies are short-lived, spanning one to three breeding seasons, the dual strategy may not have been observed if the research was conducted during years when adults did not have to work very hard to provision their chicks. As has been shown for Cory's Shearwaters *Calonectris diomedea* nesting on islands in the North Atlantic, Procellariiform foraging strategies are flexible, with populations switching from a unimodal to a bimodal strategy when adult body condition is compromised (Granadeiro *et al.* 1998).

The flexibility of the Procellariiform provisioning strategy underscores the ability of this taxon to adjust to current feeding conditions and to make decisions about where to feed when relying on distant and dispersed food resources. Our results suggest that this flexible foraging strategy is influenced by ocean productivity patterns. However, because Procellariiform seabirds may have developed a bimodal foraging strategy in response to different constraints, comparative studies are required to determine which factors influence the foraging strategy of specific populations and species. In particular, provisioning studies of sympatrically-breeding taxa and allopatric populations of the same species may be especially insightful. In addition to manipulation experiments (Weimerskirch *et al.* 1995, Bolton 1995b), interannual (e.g., El Niño) and longer-term (e.g., global warming) oceanographic variability provide opportunities to conduct natural experiments of the influence of ocean productivity and prey dispersion patterns on Procellariiform foraging strategies. In particular, if the productivity of the world's oceans is decreasing due to enhanced warming of near-surface waters (Levitus *et al.* 2000, Gregg & Conkright 2002), we may witness a greater number of Procellariiform seabirds employing a flexible bimodal foraging strategy in the future.

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REFERENCES

ASHMOLE, N.P. 1971. Seabird ecology and the marine environment. In: Farner, D.S. and King, J.R. (Eds.), *Avian Biology*, Vol. 1: 223-286. London, Academic Press.

BADUINI, C.L. 2002. Parental provisioning patterns of Wedge-tailed Shearwaters and their relation to chick body condition. *Condor* 104: 823-831.

BERROW, S.D., HUMPIDGE, R. & CROXALL, J.P. 2000. Influence of adult breeding experience on growth and provisioning of Wandering Albatross *Diomedea exulans* chicks at South Georgia. *Ibis* 142: 199-207.

BOLTON, M. 1995a. Food delivery to nestling storm-petrels: limitation or regulation? *Functional Biology* 9: 161-170.

BOLTON, M. 1995b. Experimental evidence for regulation of food delivery to storm petrel, *Hydrobates pelagicus*, nestlings: the role of chick body condition. *Animal Behaviour* 50: 231-236.

BOOTH, A.M., MINOT, E.O., FORDHAM, R.A. & IMBER, M.J. 2000. Co-ordinated food provisioning in the Little Shearwater *Puffinus assimilis haurakiensis*: a previously undescribed foraging strategy in the Procellariidae. *Ibis* 142: 144-146.

BOYER, T.P., CONKRIGHT, M.E., LEVITUS, S., STEPHENS, C., O'BRIEN, T., JOHNSON, D. & GELFELD, R. 1998. NOAA Atlas NESDIS 21, World Ocean Database 1998. Washington, U.S. Gov. Printing Office.

CATARD, A., WEIMERSKIRCH, H. & CHEREL, Y. 2000. Exploitation of distant Antarctic waters and close shelf-break waters by White-chinned Petrels rearing chicks. *Marine Ecology Progress Series* 194: 249-261.

CHAURAND, T. & WEIMERSKIRCH, H. 1994. The regular alternation of short and long foraging trips in the Blue Petrel *Halobaena caerulea*: a previously undescribed strategy of food provisioning in a pelagic seabird. *Journal of Animal Ecology* 63: 275-282.

CHAVEZ, F.P., STRUTTON, P.G., FRIEDERICH, C.E., FEELY, R.A., FELDMAN, G.C., FOLEY, D.G. & MCPHADEN, M.J. 1999. Biological and chemical response of the equatorial Pacific Ocean to the 1997-98 El Niño. *Science* 286: 2126-2131.

CHEREL, Y., BOCHER, P., TROUVE, C. & WEIMERSKIRCH, H. 2002. Diet and feeding ecology of blue petrels *Halobaena caerulea* at Iles Kerguelen, Southern Indian Ocean. *Marine Ecology Progress Series* 228: 283-299.

FERNÁNDEZ, P., ANDERSON, D.J., SIEVERT, P.R. & HUYVAERT, K.P. 2001. Foraging destinations of three low-latitude albatross (*Phoebastria*) species. *Journal of Zoology* 254: 391-404.

GORDON, H.R. & MOREL, A.Y. 1983. Remote Assessment of Ocean Color for Interpretation of Satellite Visible Imagery: a Review. New York: Springer-Verlag.

GRANADEIRO, J.P., NUNES, M., SILVA, M.C. & FURNESS, R.W. 1998. Flexible foraging strategy of Cory's Shearwater, *Calonectris diomedea*, during the chick-rearing period. *Animal Behaviour* 56: 1169-1176.

GRAY, C.M. & HAMER, K.C. 2001. Food-provisioning behaviour of male and female Manx Shearwaters, *Puffinus puffinus*. *Animal Behaviour* 62: 117-121.

GREGG, W.W. & CONKRIGHT, M.E. 2002. Decadal changes in global ocean chlorophyll. *Geophysical Research Letters* 29 (15). Article no. 1730.

HAMER, K.C. 1994. Variability and stochasticity of meal size and feeding frequency in the Little Shearwater *Puffinus assimilis*. *Ibis* 136: 271-278.

HAMER, K.C. & THOMPSON D.R. 1997. Provisioning and growth rates of nestling Fulmars Fulmarus glacialis: stochastic variation or regulation? *Ibis* 139: 31-39.

HAMER, K.C., LYNNES, A.S. & HILL, J.K. 1999. Parent-offspring interactions in food provisioning of Manx Shearwaters: implications for nestling obesity. *Animal Behavior* 57: 627-631.

HARPER P.C., CROXALL, J.P. & COOPER, J. 1985. A guide to foraging methods used by marine birds in Antarctic and Subantarctic seas. Biomass Handbook 24. 22 pp.

HEDD, A., GALES, R. & BROTHERS, N. 2001. Foraging strategies of Shy Albatross *Thalassarche cauta* breeding at Albatross Island, Tasmania, Australia. *Marine Ecology Progress Series* 224: 267-282.

HEDD, A., GALES, R. & BROTHERS, N. 2002. Provisioning and growth rates of Shy Albatross at Albatross Island, Tasmania. *Condor* 104: 12-29.

HOOKER S.B. & MCCLAIN, C.R. 2000. The calibration and validation of SeaWiFS data. *Progress in Oceanography* 45 (3-4): 427-465.

HUIN, N., PRINCE, P. & BRIGGS, D.R. 2000. Chick provisioning rates and growth in Black-browed Albatross *Diomedea melanophris* and Grey-headed Albatross *D. chrysostoma* at Bird Island, South Georgia. *Ibis* 142: 550-565.

HUNT, G.L. JR., & SCHNEIDER, D.C. 1987. Scale dependent processes in the physical and biological environment of seabirds. *In: Croxall, J.P. (Ed.), The feeding ecology of seabirds and their role in marine ecosystems*. Cambridge: Cambridge University Press. pp. 7-41.

HUNT, G.L., JR., MEHLUM, F., RUSSELL, R.W., IRONS, D., DECKER, M.B. & BECKER, P.H. 1999. Physical processes, prey abundance, and the foraging ecology of seabirds. *Proceedings International Ornithological Congress* 22: 2040-2056.

HYRENBACH, K.D., FeRNÁNDEZ, P. & ANDERSON, D.J. 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series* 233: 283-301.

KAHRU, M. & MITCHELL , B.G. 1999. Empirical chlorophyll algorithm and preliminary SeaWiFS validation for the California Current. *International Journal of Remote Sensing* 20: 3423-3429.

JOINT, J. & GROOM, S.B. 2000. Estimation of phytoplankton production from space: current status and future potential of satellite remote sensing. *Experimental Marine Biology and Ecology* 250: 233-255.

LACK, D. 1968. Ecological Adaptations for Breeding in Birds. London, Methuen.

LALLI, C.M. & PARSONS, T.R. 1997. Biological Oceanography: An Introduction. 2nd Edition. Oxford, Pergamon Press. 301 pp.

LEVITUS, S., ANTONOV, J.I., BOYER, T.P. & STEPHENS, C. 2000. Warming of the world Ocean. *Science* 287: 2225-2229.

LORENTSEN, S.H. 1996. Regulation of food provisioning in the Antarctic Petrel *Thalassoica antarctica*. *Journal of Animal Ecology* 65: 381-388.

NEL, D.C., LUTJEHARMS, J.R.E., PAKHOMOV, E.A., ANSORGE, I.J., RYAN, P.G., & KLAGES, N.T.W. 2001. Exploitation of mesoscale oceanographic features by Grey-headed Albatross *Thalassarche chrysostoma* in the southern Indian Ocean. *Marine Ecology Progress Series* 217: 15-26.

NGDC (National Geophysical Data Center). 1998. Data Announcement 88-MGG-02, Digital relief of the surface of the

Earth. Boulder: National Geophysical Data Center. (www.ngdc.noaa.gov/mgg/global/seltopo.html).

PLACE, A.R., STOYAN, N.C., RICKLEFS, R.E. & BUTLER, R.G. 1989. Physiological basis of stomach oil formation in Leach's Storm-petrel (*Oceanodroma leucorhoa*). *Auk* 106: 687-699.

PERRY, M.J. 1986. Assessing marine primary production from space. *Bioscience* 36 (7): 461-469.

PHILLIPS, R.A. & HAMER, K.C. 2000. Growth and provisioning strategies of Northern Fulmars *Fulmarus glacialis*. *Ibis* 142: 435-445.

POLOVINA, J.J., HOWELL, E., KOBAYASHI, D.R. & SEKI, M.P. 2001. The transition zone chlorophyll front, a dynamic global feature defining migration and forage habitat for marine resources. *Progress in Oceanography* 49: 469-483.

RICKLEFS, R.E. 1992. The roles of parent and chick in determining feeding rates in Leach's Storm-petrel. *Animal Behaviour* 43: 895-906.

RICKLEFS, R.E., DAY, C.H., HUNTINGTON, C.E. & WILLIAMS, J.B. 1985. Variability in feeding rate and meal size of Leach's Storm-petrel at Kent Island, New Brunswick. *Journal of Animal Ecology* 54: 883-888.

ROBY, D.D. 1991. Diet and postnatal energetics in convergent taxa of plankton-feeding seabirds. *Auk* 108: 131-146.

ROBY, D.D., BRINK, K.L. & PLACE, A.E. 1989. Relative passage rates of lipid and aqueous digesta in the formation of stomach oils. *Auk* 106: 303-313.

SHAFFER, S.A., COSTA, D.P. & WEIMERSKIRCH, H. 2001. Behavioral factors affecting foraging effort of breeding Wandering Albatrosses. *Journal of Animal Ecology* 70: 864-874.

SPRINGER, A.M., MCROY C.P. & FLINT, M.V. 1996. The Bering Sea Green Belt: shelf-edge processes and ecosystem production. *Fisheries Oceanography* 5: 205-223.

TVERAA, T., SAETHER, B.E., AANES, R. & ERIKSTAD, K.E. 1998. Regulation of food provisioning in the Antarctic petrel; the importance of parental body condition and chick body mass. *Journal of Animal Ecology* 67: 699-704.

VISWANATHAN, G.M., AFANASYEV, V., BULDYREV, S.V., MURPHY, E.J., PRINCE, P.A. & STANLEY, H.E. 1996. Levy flight search patterns of Wandering Albatrosses. *Nature* 381: 413-415.

VINOGRADOV, M.E., SHUSKINA, E.A., VEDERNIKOV, V.I., NEZLIN, N.P. & GAGARIN, V.I. 1997. Primary production and plankton stocks in the Pacific Ocean and their seasonal variation according to remote sensing and field observations. *Deep-Sea Research II* 44: 1979-2001.

WARHAM, J. 1990. The Petrels: Their Ecology and Breeding Systems. Academic Press, London. 440 pp.

WARHAM, J. 1996. The Behaviour, Population Biology, and Physiology of the Petrels. Academic Press, London. 613 pp.

WEIMERSKIRCH, H., JOUVENTIN, P. & STAHL, J.C. 1985. Comparative ecology of the six albatross species breeding on the Crozet islands. *Ibis* 128: 195-213.

WEIMERSKIRCH, H., BARTLE, J.A., JOUVENTIN, P. & STAHL, J.C. 1988. Foraging ranges and partitioning of feeding zones in three species of southern albatrosses. *Condor* 90: 214-219.

WEIMERSKIRCH, H., CHASTEL, O., ACKERMANN, L., CHAURAND, T., CUENOT-CHAILLET, F., HINDERMEYER, X. & JUDAS, J. 1994a. Alternate long and short foraging trips in pelagic seabird parents. *Animal Behaviour* 47: 472-476.

WEIMERSKIRCH, H., DONCASTER, C.P. & CUENOT-CHAILLET, K. 1994b. Pelagic seabirds and the marine environment: foraging patterns of Wandering Albatrosses in relation to prey availability and distribution. *Proceedings of the Royal Society B* 255: 91-97.

WEIMERSKIRCH, H., CHASTEL, O. & ACKERMANN, L. 1995. Adjustment of parental effort to manipulated foraging ability in a pelagic seabird, the Thin-billed Prion *Pachyptila belcheri*. *Behavior, Ecology and Sociobiology* 36: 11-16.

WEIMERSKIRCH, H., MOUGEY, T. & HINDERMEYER, X. 1997a. Foraging and provisioning strategies of Black-browed Albatrosses in relation to the requirements of the chick: natural variation and experimental study. *Behavioral Ecology* 8 (6): 635-643.

WEIMERSKIRCH, H., CHEREL, Y., CUENOT-CHAILLET, F. & RIDOUX, V. 1997b. Alternative foraging strategies and resource allocation by male and female Wandering Albatrosses. *Ecology* 78 : 2051-2063

WEIMERSKIRCH, H. 1998. How can a pelagic seabird provision its chick when relying on a distant food resource? Cyclic attendance at the colony, foraging decision and body condition in Sooty Shearwaters. *Journal of Animal Ecology* 67: 99-109.

WEIMERSKIRCH, H. & CHEREL, Y. 1998. Feeding ecology of Short-tailed Shearwaters breeding in Tasmania and foraging in the Antarctic? *Marine Ecology Progress Series* 167: 261-274.

WEIMERSKIRCH, H., PRINCE, P.A. & ZIMMERMAN, L. 2000a. Chick provisioning by the Yellow-nosed Albatross *Diomedea chlororhynchos*: response of foraging effort to experimentally increased costs and demands. *Ibis* 142: 103-110.

WEIMERSKIRCH, H., GUIONNET, T., MARTIN, J., SHAFFER, S.A., COSTA, D.P., & WILSON, R.P. 2000b. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society B* 267: 1869-1874.

WEIMERSKIRCH, H., CHASTEL, O., CHEREL, Y., HENDEN J.-A. & TVERRA, T. 2001. Nest attendance and foraging movements of northern fulmars rearing chicks at Bjornoya Barents Sea. *Polar Biology* 24: 83-88.

WEIMERSKIRCH, H. & GUIONNET, T. 2002. Comparative activity pattern during foraging of four albatross species. *Ibis* 144: 40-50.

WEIMERSKIRCH, H., ANCEL, A., CALOIN, M., ZAHARIEV, A., SPAGIARI, J., KERSTEN, M. & CHASTEL, O. 2003. Foraging efficiency and adjustment of energy expenditure in a pelagic seabird provisioning its chick. *Journal of Animal Ecology* 72: 500-508.

ZAR, J.H. 1984. Biostatistical analysis. Fourth Edition. New Jersey: Prentice-Hall. 664 pp.

EFFECTS OF THE JUAN DE FUCA EDDY AND UPWELLING ON DENSITIES AND DISTRIBUTIONS OF SEABIRDS OFF SOUTHWEST VANCOUVER ISLAND, BRITISH COLUMBIA

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SUMMARY

BURGER, A. E. 2003. Effects of the Juan de Fuca Eddy and upwelling on densities and distributions of seabirds off southwest Vancouver Island, British Columbia. *Marine Ornithology* 31: 113-122.

I compared meso-scale averages of sea surface temperature (SST) and hydroacoustic indices of prey abundance with densities of seabirds measured year-round over the continental shelf off southwest Vancouver Island, British Columbia, Canada in 1993-1996. A fixed strip transect (total length 110 km; width 300 m) was divided into six legs (lengths 14-30 km) to sample different shelf habitats. Three foraging guilds were considered: divers (dominated by Common Murres *Uria aalge* and other alcids), surface-feeders (dominated by California Gulls *Larus californicus* in summer, and other gulls year-round), and shearwaters (mainly Sooty Shearwater *Puffinus griseus*). Mean SST, prey scores, and densities of most birds (all surface-feeders and most divers) were low and similar among the 6 transect legs during winter and spring (mid-December through mid-June), but these measures all increased and differed significantly among the legs during summer and autumn (mid-June through mid-December). In summer and autumn, cold SSTs, high prey scores, and high seabird densities were consistently associated with the effects of the seasonal eddy over the Juan de Fuca canyon, whose influence spilled over the adjacent shelf. SST alone, however, did not explain the observed patterns of prey and seabird dispersion. One leg characterized by cold, upwelled water supported low prey and bird abundance, while another leg adjacent to the outer canyon had high prey and bird abundance, but SST was not consistently low. These results suggest that SST alone (such as satellite imagery) cannot be used to predict seabird distribution in this area. The interactions of bathymetry, ocean currents, and physical conditions of seabirds and their prey need to be more clearly understood in this area before reliable predictions of seabird distributions based on satellite imagery are possible.

Keywords: continental shelf, Juan de Fuca Eddy, seabird densities, seasonal variations, upwelling, Vancouver Island

INTRODUCTION

Associations of seabirds with coarse- or meso-scale (1-100 km) physical processes in the ocean have been described from several parts of the world (Haney 1986, Hunt & Schneider 1987, Schneider 2002). Some meso-scale patterns have been described for seabird distributions in the northeast Pacific (Wahl *et al.* 1989, 1993), but the effects of oceanic processes over the continental shelf in this area are not well understood (Vermeer *et al.* 1987, 1989, Hay 1992, Logerwell & Hargreaves 1996). Understanding the distribution and abundance of seabirds relative to meso-scale ocean processes is important for several reasons. This spatial range covers the daily foraging range (ambit) of most seabirds. Moreover, several of the dynamic physical processes responsible for increased productivity and aggregations of prey are most evident at scales of 10s of km, but less evident at spatial scales smaller or larger than this range (Hunt & Schneider 1987, Schneider 2002). These physical processes include the effects of large ocean eddies, wind-induced upwelling plumes, broad oceanic fronts, island wakes, and tidal fronts.

Another reason for studying seabird distributions at meso-scales is that currents, eddies and upwelling plumes can be readily identified and tracked using satellite imagery at this spatial scale. Satellite imagery, predominantly of sea surface temperatures (SST), has been used to characterize ocean habitats of seabirds in a few studies (e.g., Briggs *et al.* 1987, Haney 1986, 1989a, b). Understanding the distribution of seabirds in relation to SST or other remotely-sensed parameter is needed before satellite imagery can be reliably used to predict the distribution of seabirds. Satellite images could be a valuable tool in predicting the distribution of seabirds in the event of a major oil spill. Knowing the likely distribution and relative densities of seabirds would help assess the likely risks from the spill, allow containment efforts to be directed to the most critical areas, and determine where aerial surveillance and other monitoring efforts should be concentrated.

The continental shelf off southwest Vancouver Island is a highly productive marine zone, which provides foraging opportunities for tens of thousands of seabirds (Vermeer *et al.* 1987, 1989, 1992, Hay 1992, Wahl *et al.* 1993, Logerwell & Hargreaves 1996). There is also a high risk of a major oil spill in the area, from many oil tankers and other large vessels transiting the Strait of Juan de Fuca to or from Seattle, Vancouver, and other large ports nearby (Cohen & Aylesworth 1990, Burger 1992). This paper, part of a series on the distribution, densities and species composition of seabirds off southwest Vancouver Island (Burger 2002a, Burger *et al.* in press), reports on the meso-scale distribution of seabirds recorded year-round along a 110 km transect route over the continental shelf (Fig. 1). Analysis focused on the likely effects of two powerful physical processes affecting sea temperatures, productivity and prey distribution: wind-induced upwelling along the inner continental shelf, and upwelling generated by the Juan de Fuca Eddy. In particular, this paper examines the distribution of the major groups of seabirds relative to sea surface temperatures. Besides improving our understanding of the biology of seabirds in this area, this is an important step towards using satellite imagery to monitor the likely distribution and abundance patterns of seabirds in this area.

STUDY AREA AND OCEAN PROCESSES

The continental shelf (delineated by depths less than 200 m) extends to approximately 50 km off the coast of southwest Vancouver Island (Thomson 1981, Freeland 1992). The shelf is cut by several deep canyons perpendicular to the shore, which create conditions favourable to upwelling of cold, nutrient-rich water (Denman *et al.* 1981, Allen *et al.* 2001). The largest of these is the Juan de Fuca Canyon, extending seaward from the Strait of Juan de Fuca (Fig. 1). During the summer a large anti-clockwise (cyclonic) eddy develops over this canyon at the mouth of the strait, which is responsible for massive upwelling of deep, nutrient-rich water (Thomson *et al.* 1989, Freeland & Denman 1982, Freeland 1992). This upwelled water spills over the southern edge of the continental shelf, creating a large pool of colder surface water over Swiftsure Bank and beyond. The effects of the eddy are clearly visible from satellite images of sea surface temperature (Fig. 2). Parts of the shelf area affected by the eddy are productive foraging grounds for birds, fish and whales, as well as commercially important fishing grounds (Healy *et al.* 1990, Vermeer *et al.* 1992).

Wind-induced upwelling over the shelf also affects the local hydrography and is evident at the sea surface. During summer, the prevailing northwest winds combined with the Coriolis force drag the surface water offshore, resulting in plumes of cold upwelled water moving seaward from the inner shelf (Thomson 1981, Freeland 1992). During winter, the prevailing southeast winds force surface water shoreward, inhibiting upwelling over the inner shelf. Chlorophyll and zooplankton densities over the shelf off southwest Vancouver Island are consequently highly seasonal, with winter densities about one tenth of summer values (Thomas & Emery 1986, Mackas 1992).

METHODS

Sea surface temperature (SST), hydroacoustic measures of prey abundance, and densities of birds were recorded from a moving vessel along a 110 km fixed transect route (Figure 1). The transect was designed to include a range of marine habitats on the continental shelf that could be traversed in a day's cruise. The transect was divided into six legs of unequal length. The two portions parallel with the shore (Inshelf and Offshelf) were both divided into two legs in order to compare areas proximal (Inshelf East: mean distance 14.0 ± SE 0.1 km; and Offshelf East: 14.3 ± 0.3 km) and distal (Inshelf West: 14.5 ± 0.4 km; and Offshelf West: 21.6 ± 0.6 km) to the canyon at two distances offshore. The Canyon leg (16.3 ± 0.5 km) covered the water from the edge of the canyon to the deepest portion (> 200 m). The Cross-shelf leg (29.6 ± 1.0 km) ran perpendicular to the shore and the depth isobars. The outer shelf legs were truncated on two winter/spring surveys due to limited daylength and on one summer/autumn survey due to mechanical problems.

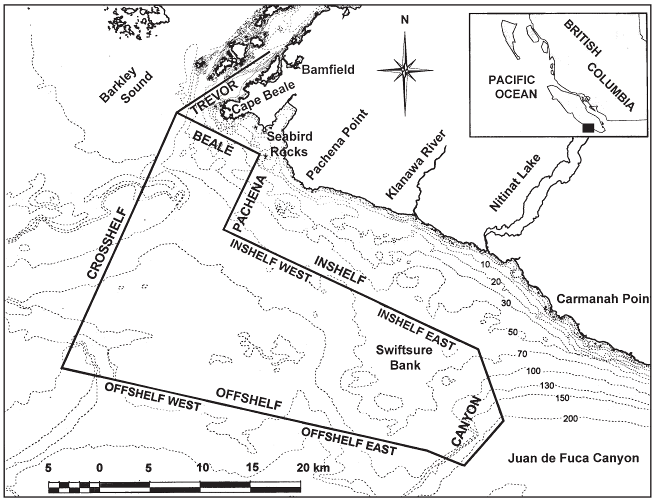

Fig. 1. Map of the study area showing the transect route. This analysis used data from the Inshelf (East and West), Canyon, Offshelf (East and West), and Cross-shelf legs. Depth isobaths are in metres.

Surveys were conducted aboard the 11 m research vessel M.V. *Alta* (eye-level 2.0-2.5 m above the sea), and occasionally from other similar vessels, and used LORAN and Global Positioning System (GPS) for navigation. Vessel speed was relatively constant (mean 14.8 km h^{-1}, range 13.0-18.5 km h^{-1}). The vessel was occasionally slowed to permit counting and identification of birds in dense flocks. Occasional deviations off-course to investigate flocks of birds were excluded from the data. All data were collected in 1-minute bins, corresponding to about 250-280 m of travel. Surveys were usually restricted to periods when the Beaufort sea state was 3 or less (winds <5.5 m s^{-1} and white-caps from breaking wavelets rare), but sometimes included brief periods of stronger winds to maintain continuity.

Sea surface temperatures (accurate to 0.1° C) were manually recorded from a hull-mounted electronic thermometer in 1993, and automatically in a flow-through system using an Endeco YSI PC600 probe linked to a computer in 1994-1996. Both systems sampled the water about 1 m below the surface. To illustrate the variations in temperature among the legs within the entire transect,

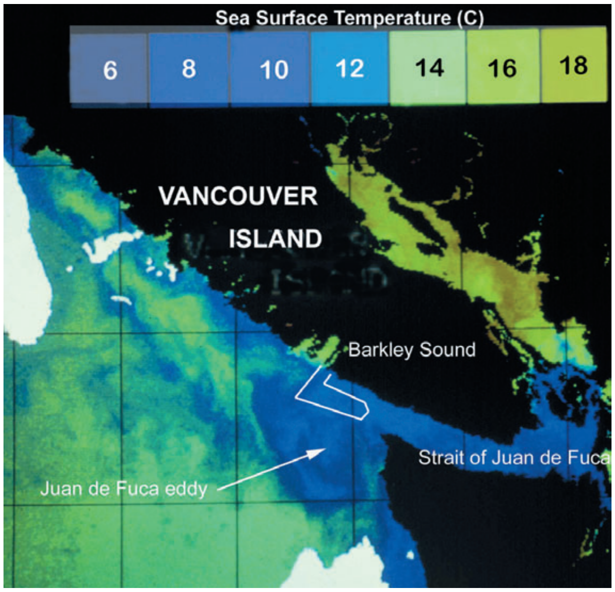

Fig. 2. Satellite image of sea surface temperature (°C) off southwest Vancouver Island on 18 August 1982. Several features typical of summer conditions can be seen, including cold, upwelled water associated with the Juan de Fuca Eddy and the plumes of colder water upwelled over the shelf. The transect route is shown.

I calculated a deviation function on each day surveyed, which was the difference between the mean temperature within each leg and the mean for the transect as a whole on that day. Positive deviations indicate warmer temperatures and negative deviations colder temperatures within the leg than for the transect as a whole.

Prey abundance was measured using a 200 kHz Furuno 600 hull-mounted sounder (approx. 1 m deep), with a paper trace recorder. Sounder traces were divided into 1 minute intervals of travel (250-280 m) and 10 m depth intervals. Within each rectangle formed by this division observers visually scored the density of prey, based on the intensity of the sounder trace, using a scale of 0 (no prey) through 9 (near-saturation; Piatt 1990). Three independent observers gave almost identical scores in tests of the same sounder traces. I then squared the score to account for the non-linear change in sounder intensity relative to prey school density (Forbes & Nakken 1972). Analysis focused on the 1-10 m depth range, as a measure of near-surface prey likely to be accessible to surface-feeding birds, and the 1-40 m range, as a measure of the overall prey abundance and the prey accessible to most diving birds. A few surveys which sampled deeper depths showed few schools of fish below 40 m, other than Pacific hake *Merluccius productus*, which were not taken by birds except as fisheries discards (Hay *et al.* 1992, AEB. pers. obs.).

I did not attempt to identify the organisms producing each sounder trace, but schooling fish (predominantly immature herring *Clupea harengus pallasi* and sand lance *Ammodytes hexapterus*) and euphausiids (predominantly *Thysanoessa spinifera* and *Euphausia pacifica*) are common in the study area within the depths sampled (Hay *et al.* 1992, Mackas & Galbraith 1992). Traces made by larger fish not taken by birds, such as salmonids and spiny dogfish *Squalus acanthias*, could usually be identified by the solitary, bold traces, and were disregarded. The interpretation of sounder traces excluded near-surface interference caused by waves and diffuse back-scatter from small plankton, but included dense schools of larger zooplankton, primarily euphausiids (Mackas & Galbraith 1992; AEB pers. obs.).

Two observers reported birds within an area 250 m ahead, and 150 m on either side of the vessel (transect width was 300 m). Data were recorded manually by a third person. Several observers took turns on duty to avoid fatigue. Densities were calculated from the area of the strip covered in each leg, on each day surveyed. To focus on birds most likely to be foraging, I considered only birds seen on the water with the exception of storm-petrels, which frequently forage on the wing. Storm-petrels on the water and flying were both included in analyses.

Birds were grouped into three foraging guilds: divers, surface-feeders, and shearwaters. Diving birds included loons, cormorants, grebes, and alcids. Surface-feeding birds included fulmars, storm-petrels, phalaropes, gulls, and jaegers. Shearwaters, which usually forage at the surface but are also accomplished divers (Burger 2001), were treated as a separate foraging guild. Separate analyses were done for the most common species (mean density >0.5 birds km^{-2} and found in at least 50% of surveys). The remaining less common species were not analysed separately, but were included in the appropriate foraging guilds. An exception was made for Marbled Murrelets *Brachyramphus marmoratus*: although uncommon it was included in the detailed analysis because it is a threatened species in British Columbia and the United States, and its seasonal use of shelf and offshore waters is poorly documented (Burger 2002b).

Seasons were defined as: winter – 16 December through 15 March; spring – 16 March – 15 June; summer – 16 June – 15 September; autumn – 16 September – 15 December (Morgan *et al.* 1991). Based on the changes in SST (see results), I pooled the winter/spring data, and the summer/fall data.

The bird and prey data presented problems for statistical analysis, because of the high variability, heteroscedacity, and occurrence of many zeroes. Logarithmic transformations (Zar 1996) did not completely eliminate these problems. Consequently, I used non-parametric Kruskal-Wallis analysis of variance to compare data from the different legs, using SPSS 10.0. Tests were considered significant if P<0.05.

RESULTS

Sea surface temperatures

Variations in SST among the six legs of the transect showed a strong seasonal pattern (Fig. 3). During winter and most of the spring there were relatively few differences in temperature among the legs, with the warmest waters often over the Canyon. From June through mid-December, however, the mean temperatures within each leg showed clear differences, often exceeding 2°C. During this period, the two legs along the inner shelf (Inshelf East and Inshelf West) and the Canyon leg had consistently colder SST than the legs on the outer shelf and the Cross-shelf leg. This was consistent with summer upwelling associated with the Juan de Fuca Eddy. The cold temperatures in the Inshelf West leg also indicated upwelling over the inner shelf, which was probably a combination of the effects of wind forcing and the eddy. To match the two seasonal temperature regimes, the prey and bird data were pooled into winter/spring and summer/autumn periods for statistical analyses.

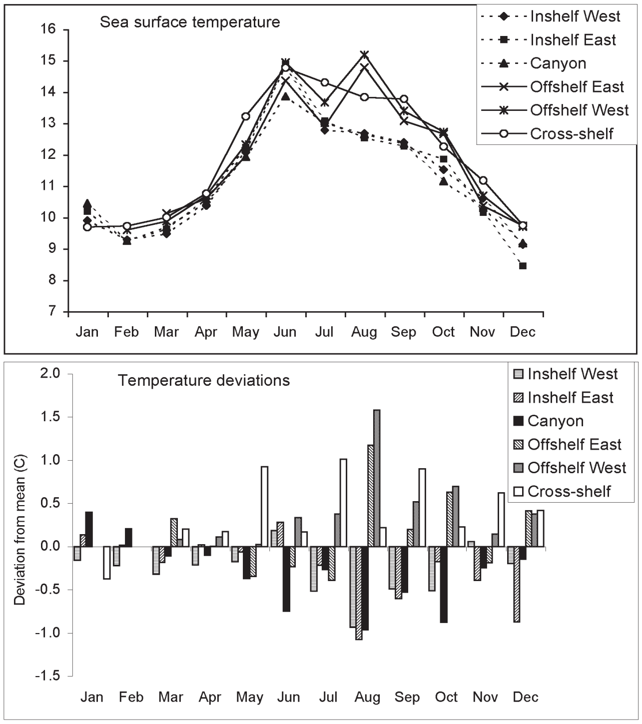

Fig. 3. Monthly variations in sea surface temperatures within each transect leg, showing mean temperatures (a), and mean deviation in temperature within each leg, relative to the mean for the whole transect on each day of survey (b). Positive deviations indicate warmer temperatures and negative deviations colder temperatures.

Prey abundance

Prey abundance scores varied seasonally, and were lowest in winter and highest in summer and autumn (Fig. 4). The greatest increases occurred in the two legs immediately adjacent to the canyon and, in autumn, in the Canyon leg itself. When prey scores were grouped into two seasons, the differences among the six transect legs were not significant in winter/spring, but were significant in summer/autumn for the 0-40 m depth range, and nearly so for the 0-10 m depth range (Table 1).

Bird densities

The bird species recorded, mean year-round densities and percentage occurrence in transects are summarised in Table 2. Seasonal trends within the transect are given elsewhere (Burger 2002a, Burger *et al.* in press.). This analysis focused on seasonal differences among the legs in the occurrence (Table 3) and densities (Table 4) of the more common species and groups.

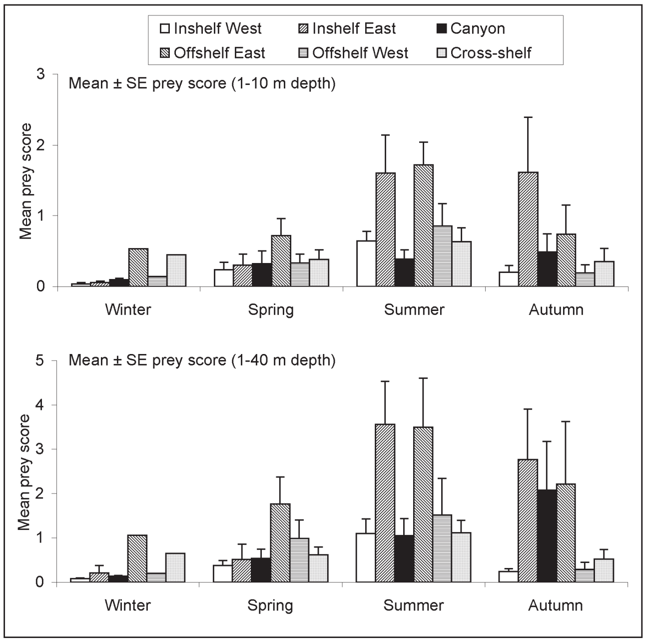

Fig. 4. Mean (± SE) of the hydroacoustic prey scores per transect leg in each season, within the near-surface 1-10 m depth range (a), and the 1-40 m depth range (b).

Loons and cormorants – Pelagic Cormorants *Phalacrocorax pelagicus*, Brandt's Cormorants *P. penicillatus* and Pacific Loons *Gavia pacifica* were uncommon on the shelf water (Table 2). They occurred in all legs (Table 3) but had higher densities in the legs nearest the shore (Table 4). Densities did not differ significantly among the legs in winter/spring but in summer/autumn there were significantly more birds in the three legs over or adjacent to the canyon (Table 4).

Common Murre *Uria aalge* – Murres were found in nearly every leg in all seasons (Tables 3) and had the highest densities among the diving birds (Tables 2 and 4). Densities were considerably higher in summer/autumn than in winter/spring, but did not vary significantly among the six legs in either of the seasonal periods. During summer/autumn, however, the highest densities occurred in the two legs immediately adjacent to the canyon (Inshelf East and Offshelf East).

Cassin's Auklet *Ptychoramphus aleuticus* – This species occurred in about half of the surveys in each leg (Table 3). Densities were higher in summer/autumn than in winter/spring (Table 4). There were no significant differences in density among the legs in winter/spring, but during summer/autumn the densities were significantly higher in the three legs over or adjacent to the canyon.

Marbled Murrelet – This species, included here because of its threatened status, was rare over the shelf during winter/spring and usually absent during summer/autumn (Tables 2-4). There were no significant differences in density among the legs, but the data were too sparse for rigorous tests.

Rhinoceros Auklet *Cerorhinca monocerata* – This species was more common over the shelf during winter/spring than summer/fall and was found in all legs (Tables 3 and 4). During winter/spring Rhinoceros Auklets had similar densities in all six legs, but during summer/autumn they were concentrated in the three legs over or adjacent to the canyon.

Shearwaters – Sooty Shearwaters *Puffinus griseus* were by far the most common shearwater in the study area followed by Short-tailed Shearwaters *P. brevirostris* and other species (Table 2). Some Short-tailed Shearwaters were undoubtedly recorded as Sooty

TABLE 1
Mean (± SE) prey scores within each transect leg, grouped into two seasons.
Prey scores for the near-surface depths (1-10 m) and for the entire sample (1-40 m) are shown.

Leg	1-10 m depth		1-40 m depth		No. of surveys	
	Winter + Spring	Summer + Autumn	Winter + Spring	Summer + Autumn	Winter + Spring	Summer + Autumn
Inshelf West	0.18 ± 0.08	0.42 ± 0.11	0.29 ± 0.09	0.67 ± 0.23	10	8
Inshelf East	0.23 ± 0.12	1.61 ± 0.44	0.42 ± 0.25	3.16 ± 0.71	7	8
Canyon	0.26 ± 0.13	0.44 ± 0.13	0.42 ± 0.17	1.56 ± 0.57	7	8
Offshelf East	0.68 ± 0.20	1.23 ± 0.31	1.65 ± 0.50	2.85 ± 0.86	6	8
Offshelf West	0.30 ± 0.11	0.52 ± 0.20	0.85 ± 0.37	0.90 ± 0.45	6	8
Cross-shelf	0.40 ± 0.10	0.49 ± 0.14	0.62 ± 0.14	0.81 ± 0.20	5	8
Kruskal-Wallis test (df = 5 for all)						
Chi-square	7.54	10.56	7.70	16.86		
P	0.184	0.061	0.173	0.005		

TABLE 2
Summary of year-round mean densities and percentage occurrence of seabird species recorded in 29 surveys made between May 1993 and December 1995 over the shelf off southwest Vancouver Island.

Taxa	Scientific name	Density (birds km^{-2})			Percentage occurrence in surveys	Maximum count
		Mean	SE	% of total		
Red-throated Loon	*Gavia stellata*	0.010	0.009	0.019	7	2
Pacific Loon	*Gavia pacifica*	0.272	0.064	0.498	69	39
Common Loon	*Gavia immer*	0.012	0.007	0.021	14	1
Loon spp.		0.094	0.050	0.172	31	35
Western Grebe	*Aechmophorus occidentalis*	0.015	0.008	0.027	14	5
Black-footed Albatross	*Phoebastria nigripes*	0.025	0.013	0.046	21	7
Northern Fulmar	*Fulmarus glacialis*	3.842	1.314	7.033	76	999
Pink-footed Shearwater	*Puffinus creatopus*	0.049	0.024	0.089	34	22
Buller's Shearwater	*Puffinus bulleri*	0.014	0.008	0.026	17	5
Sooty Shearwater	*Puffinus griseus*	10.852	2.358	19.865	83	1690
Short-tailed Shearwater	*Puffinus tenuirostris*	0.165	0.076	0.302	62	58
Fork-tailed Storm-petrel	*Oceanodroma furcata*	1.348	0.574	2.467	59	489
Leach's Storm-petrel	*Oceanodroma leucorrhoa*	0.004	0.004	0.007	3	4
Brant's Cormorant	*Phalacrocorax penicillatus*	0.342	0.170	0.626	72	160
Pelagic Cormorant	*Phalacrocorax pelagicus*	0.066	0.021	0.121	52	7
Cormorant spp.		0.010	0.004	0.019	17	3
Surf Scoter	*Melanitta perspicillata*	0.296	0.168	0.541	34	172
White-winged Scoter	*Melanitta fusca*	0.066	0.031	0.120	31	25
Black Scoter	*Melanitta nigra*	0.055	0.039	0.100	7	35
Scoter spp.		0.138	0.061	0.252	34	41
Other waterfowl*		0.337	0.187	0.617	31	173
Red-necked Phalarope	*Phalaropus lobatus*	1.192	0.889	2.182	48	902
Red Phalarope	*Phalaropus fulicaria*	0.049	0.038	0.090	10	39
Phalarope spp.		0.293	0.115	0.536	45	76
Pomarine Jaeger	*Stercorarius pomarinus*	0.031	0.013	0.058	21	9
Parasitic Jaeger	*Stercorarius parasiticus*	0.003	0.002	0.005	10	1
Jaeger spp.		0.002	0.002	0.004	7	1
Bonaparte's Gull	*Larus philadelphia*	0.012	0.008	0.022	10	7
Mew Gull	*Larus canus*	0.141	0.089	0.257	21	86
Ring-billed Gull	*Larus delawarensis*	0.006	0.004	0.011	7	4
California Gull	*Larus californicus*	16.698	7.325	30.567	79	6975
Herring Gull	*Larus argentatus*	0.288	0.185	0.527	52	184
Thayer's Gull	*Larus thayeri*	0.153	0.067	0.279	28	57
Western Gull	*Larus occidentalis*	0.041	0.009	0.076	59	5
Glaucous-winged Gull	*Larus glaucescens*	4.444	0.826	8.135	100	708
Black-legged Kittiwake	*Rissa tridactyla*	0.506	0.264	0.927	31	220
Sabine's Gull	*Xema sabini*	1.312	0.659	2.402	31	539
Gull spp.		0.586	0.249	1.072	69	171
Common Murre	*Uria aalge*	7.774	1.444	14.230	100	904
Pigeon Guillemot	*Cepphus columba*	0.030	0.013	0.055	28	10
Marbled Murrelet	*Brachyramphus marmoratus*	0.130	0.044	0.239	52	19
Ancient Murrelet	*Synthliboramphus antiquus*	0.062	0.033	0.113	17	26
Cassin's Auklet	*Ptychoramphus aleuticus*	1.937	0.737	3.546	79	686
Rhinoceros Auklet	*Cerorhinca monocerata*	0.852	0.186	1.559	93	106
Tufted Puffin	*Fratercula cirrhata*	0.038	0.025	0.070	24	5
Alcid spp.		0.037	0.017	0.067	24	11
Total birds		54.63	59.16	100.0	100	10396

* Single sightings of lone Harlequin Duck (*Histrionicus histrionicus*) and Red-breasted Merganser (*Mergus serrator*), and a flock of 31 Brant (*Branta bernicla*).

Shearwater due to difficulties in distinguishing these species. Shearwaters were rare during the winter (those identified were predominantly Short-tailed Shearwaters) but more common in other seasons (Table 3). Densities of shearwaters showed no significant differences among legs in either of the seasonal periods, but there were seasonal shifts in distribution (Table 4). During winter/spring most shearwaters were found on the outer shelf legs and the outer portion of the Cross-shelf leg. In summer/autumn, however, most were in the three legs over or adjacent to the canyon, with the highest densities in the Inshelf East leg.

Northern Fulmar *Fulmarus glacialis* – Fulmars were rare in winter and spring (Tables 3 and 4). During summer/autumn they showed no significant variation in density among the transects, but somewhat higher numbers over or near the canyon and in the Offshelf West.

Fork-tailed Storm-petrel *Oceanodroma furcata* – This species was found in low numbers year-round (Tables 2-4). During winter/spring there were no significant differences in density and many were found in the Cross-shelf leg. Densities differed among legs in summer/autumn, with most birds in the Offshelf West leg.

Gulls – Gulls were by far the most common surface-feeders. Glaucous-winged Gulls *Larus glaucescens* occurred year-round and in all legs (Table 2 and 3), with similar densities among legs in winter/spring, but significantly higher densities in the Inshelf East and Canyon legs in summer (Table 4). California Gulls *L. californicus* were rare and relatively uniformly distributed in winter/spring, but were the most common bird during the summer and autumn surveys and huge flocks were found associated with the canyon, especially in the Inshelf East leg (Table 4). Other gull species, notably Mew Gull *L. canus*, Thayer's Gull *L. thayeri*, Black-legged Kittiwakes *Rissa tridactyla* and Sabine's Gull *Xema sabini* were seasonally common, but not reported sufficiently often for detailed analysis (Table 2). Total counts of gulls, dominated by California Gulls, were relatively uniformly distributed in winter/spring but strongly concentrated in the Inshelf East and Canyon legs in summer/autumn (Table 4).

Comparison of foraging guilds

Pooled data for all diving birds and surface-feeders largely mirror the patterns of the most abundant species in each guild, namely Common Murres and California Gulls, respectively (Tables 3 and 4). Both guilds showed seasonal shifts in density and distribution, from low-density, relatively uniform distributions in winter/spring to high-density aggregations in the Inshelf East and Canyon legs, and, in the case of the diving birds, also in the Offshelf East leg (Fig. 5). Shearwaters, as described above, were concentrated over the outer shelf in winter/spring and had a distribution similar to the divers in summer/autumn (Fig. 5). The spatial distribution of seabirds overall was largely influenced by shearwaters in winter/spring and California Gulls in summer/autumn (Fig. 5, Table 4).

TABLE 3
Proportion of surveys in which each species or group of birds was recorded within each transect leg.

	Most affected by canyon and eddy											
	Inshelf West		Inshelf East		Canyon		Offshelf East		Offshelf West		Cross-shelf	
Species or group of birds	winter & spring	summer & autumn	winter & spring	summer & autumn	winter & spring	summer & autumn	winter & spring	summer & autumn	winter & spring	summer & autumn	winter & spring	summer & autumn
Diving birds												
Loons & cormorants	0.44	0.67	0.56	0.75	0.44	0.83	0.43	0.27	0.43	0.18	0.78	0.50
Common Murre	1.00	0.92	1.00	1.00	1.00	0.83	1.00	0.91	1.00	1.00	0.89	1.00
Cassin's Auklet	0.44	0.42	0.67	0.67	0.44	0.75	0.57	0.73	0.57	0.55	0.56	0.42
Marbled Murrelet	0.11	0.00	0.11	0.17	0.22	0.00	0.00	0.00	0.00	0.00	0.22	0.17
Rhinoceros Auklet	0.78	0.42	0.67	0.75	0.67	0.58	0.29	0.45	0.57	0.09	0.78	0.50
Other alcids	0.11	0.25	0.11	0.17	0.44	0.25	0.43	0.36	0.00	0.00	0.33	0.33
Shearwaters (all species)	0.78	0.92	0.56	0.92	0.56	0.83	1.00	0.91	0.86	0.91	0.89	0.92
Surface-feeders												
Northern Fulmar	0.22	0.58	0.11	0.83	0.00	0.58	0.00	0.82	0.00	1.00	0.33	0.92
Fork-tailed Storm-petrel	0.00	0.00	0.11	0.08	0.33	0.00	0.29	0.18	0.43	0.45	0.22	0.33
Other procellariiforms	0.00	0.08	0.00	0.17	0.00	0.08	0.00	0.27	0.29	0.45	0.22	0.33
California Gull	0.44	1.00	0.56	0.92	0.56	0.92	0.43	1.00	0.43	0.91	0.67	1.00
Glaucous-winged Gull	1.00	0.92	1.00	1.00	1.00	1.00	1.00	1.00	1.00	0.91	1.00	0.83
Other gulls	0.67	0.75	0.67	0.75	0.78	0.67	0.29	0.82	0.57	0.64	0.78	0.75
No. of surveys	9	12	9	12	9	12	7	11	7	11	9	12

TABLE 4
Mean (± SE) densities (Birds km^2) of birds recorded within each transect leg off southwest Vancouver Island.
The data are grouped into two seasons: winter+spring (when the canyon eddy effect was absent or weak), and summer-autumn (when the effect was strongest). Densities were calculated from birds seen on the water, except for Fork-tailed Storm Petrels for which both birds on the water and flying were included. The number of surveys in each leg is given in Table 3.

			Most affected by canyon and eddy					Kruskal-Wallace test (df = 5 for all)	
Bird groups and species	Season	Inshelf West	Inshelf East	Canyon	Outshelf East	Outshelf West	Crossshelf	Chi-sq.	P
Diving birds									
Loons & Cormorants	Winter+Spring	0.24 ± 0.24	0.03 ± 0.03	0.05 ± 0.03	0.03 ± 0.03	0.00 ± 0.00	0.03 ± 0.03	1.588	0.903
Loons & Cormorants	Summer+Autumn	0.07 ± 0.07	0.30 ± 0.14	0.37 ± 0.16	0.22 ± 0.22	0.00 ± 0.00	0.01 ± 0.01	12.850	0.025
Common Murre	Winter+Spring	1.21 ± 0.33	1.98 ± 1.27	1.45 ± 0.50	4.42 ± 1.85	0.56 ± 0.23	2.65 ± 1.09	8.573	0.127
Common Murre	Summer+Autumn	6.11 ± 2.94	16.14 ± 5.52	5.90 ± 3.38	13.09 ± 6.98	5.30 ± 1.97	7.35 ± 2.21	6.494	0.261
Cassin's Auklet	Winter+Spring	0.26 ± 0.17	0.48 ± 0.13	0.22 ± 0.11	0.99 ± 0.41	0.06 ± 0.04	0.13 ± 0.06	7.065	0.216
Cassin's Auklet	Summer+Autumn	0.34 ± 0.24	10.79 ± 7.43	4.81 ± 1.99	4.85 ± 2.61	0.16 ± 0.09	0.22 ± 0.12	13.539	0.019
Marbled Murrelet	Winter+Spring	0.05 ± 0.05	0.05 ± 0.05	0.09 ± 0.06	0.00 ± 0.00	0.00 ± 0.00	0.16 ± 0.13	3.534	0.618
Marbled Murrelet	Summer+Autumn	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.00 ± 0.00	0.01 ± 0.01	4.833	0.437
Rhinoceros Auklet	Winter+Spring	0.54 ± 0.22	0.85 ± 0.37	0.90 ± 0.41	0.27 ± 0.18	0.54 ± 0.22	0.64 ± 0.33	2.659	0.752
Rhinoceros Auklet	Summer+Autumn	0.05 ± 0.05	0.20 ± 0.10	0.25 ± 0.09	0.34 ± 0.21	0.00 ± 0.00	0.04 ± 0.02	11.314	0.045
All diving birds	Winter+Spring	2.41 ± 0.71	3.39 ± 1.26	2.77 ± 0.63	5.75 ± 1.98	1.17 ± 0.28	3.66 ± 1.17	7.555	0.183
All diving birds	Summer+Autumn	6.59 ± 3.02	27.66 ± 12.23	11.53 ± 3.43	18.73 ± 8.97	5.46 ± 2.02	7.63 ± 2.23	7.606	0.179
Shearwaters									
Sooty and Short-tailed	Winter+Spring	0.75 ± 0.46	0.93 ± 0.61	0.23 ± 0.18	23.54 ± 15.92	10.63 ± 7.59	5.60 ± 3.95	6.484	0.262
Sooty and Short-tailed	Summer+Autumn	1.21 ± 0.66	27.98 ± 19.51	7.58 ± 4.97	18.55 ± 13.81	5.57 ± 2.24	1.97 ± 0.96	5.691	0.337
Surface-feeders									
Northern Fulmar*	Winter+Spring	0	0	0	0	0	0	-	-
Northern Fulmar	Summer+Autumn	0.20 ± 0.10	4.38 ± 4.02	13.69 ± 13.16	0.93 ± 0.44	3.17 ± 1.83	1.52 ± 0.95	3.558	0.615
Fork-tailed Storm Petrel	Winter+Spring	0.00 ± 0.00	0.03 ± 0.03	0.46 ± 0.33	0.31 ± 0.24	0.36 ± 0.22	6.53 ± 6.47	5.687	0.338
Fork-tailed Storm Petrel	Summer+Autumn	0.00 ± 0.00	0.02 ± 0.02	0.00 ± 0.00	0.08 ± 0.07	4.42 ± 2.90	0.70 ± 0.47	14.748	0.011
California Gull	Winter+Spring	0.37 ± 0.32	0.03 ± 0.03	0.03 ± 0.03	0.00 ± 0.00	0.46 ± 0.46	0.26 ± 0.13	8.959	0.111
California Gull	Summer+Autumn	1.98 ± 0.84	268.86 ± 145.76	36.45 ± 20.17	12.13 ± 4.92	6.57 ± 3.55	0.90 ± 0.40	13.781	0.017
Glaucous-winged Gull	Winter+Spring	1.23 ± 0.40	1.08 ± 0.39	1.16 ± 0.37	3.33 ± 0.90	0.91 ± 0.26	1.44 ± 0.58	5.332	0.377
Glaucous-winged Gull	Summer+Autumn	0.79 ± 0.32	16.52 ± 10.66	10.36 ± 7.28	2.77 ± 0.99	0.33 ± 0.12	0.12 ± 0.04	19.028	0.002
All gulls	Winter+Spring	2.32 ± 1.15	1.32 ± 0.41	1.43 ± 0.36	4.83 ± 2.03	5.24 ± 4.21	2.79 ± 1.15	3.135	0.679
All gulls	Summer+Autumn	3.12 ± 0.94	286.96 ± 148.94	51.16 ± 30.32	21.79 ± 6.93	10.25 ± 6.47	1.24 ± 0.40	21.251	0.001
All surface-feeders	Winter+Spring	2.32 ± 1.15	1.32 ± 0.41	1.45 ± 0.35	4.83 ± 2.03	5.30 ± 4.22	4.55 ± 1.78	4.236	0.516
All surface-feeders	Summer+Autumn	3.32 ± 1.01	291.43 ± 151.31	64.85 ± 43.27	22.78 ± 7.21	14.99 ± 6.36	2.87 ± 1.04	16.978	0.005
All birds									
All birds on water	Winter+Spring	5.50 ± 1.67	5.82 ± 1.89	4.55 ± 0.92	34.39 ± 17.83	17.44 ± 7.77	14.44 ± 5.53	10.648	0.059
All birds on water	Summer+Autumn	17.04 ± 7.48	348.93 ± 168.08	84.16 ± 43.64	62.64 ± 15.51	28.79 ± 9.59	12.79 ± 3.23	14.359	0.013
All birds on water + flying	Winter+Spring	18.94 ± 3.88	14.55 ± 2.73	13.88 ± 2.31	68.40 ± 39.79	29.92 ± 9.20	31.15 ± 11.44	8.035	0.154
All birds on water + flying	Summer+Autumn	40.38 ± 11.06	451.53 ± 201.04	139.29 ± 48.34	92.03 ± 16.27	58.25 ± 12.87	27.47 ± 5.04	14.782	0.011

* Northern Fulmar were not observed on the water during winter/spring and very few were seen flying.

DISCUSSION

Processes affecting seabirds on the shelf

Seabird distributions on the continental shelf off southwest Vancouver Island are affected by several physical and biological processes, and by fishing vessels (Martin & Myres 1969, Porter & Sealy 1981, Vermeer *et al.* 1989, Hay 1992, Logerwell & Hargreaves 1996). This study focused on upwelling processes affecting near-surface temperatures and hence SST visible on satellite images. Water temperatures recorded in the transects during the summer and autumn showed evidence of wind-induced upwelling over the inner shelf (Denman *et al.* 1981, Thomson 1981, Thomson *et al.* 1989), and upwelling associated with the large Juan de Fuca Eddy (Freeland & Denman 1982, Freeland 1992). The relatively low SST in the Inshelf East and Inshelf West legs in summer/autumn was likely the result of both processes, with decreasing influence of the Juan de Fuca Eddy in the western leg. Low temperatures in the Canyon leg were likely due to the effects of the eddy. More detailed measurements of the temperature, salinity and nutrient contents of the water are necessary to determine the origins of the cold surface water.

Aggregations of seabirds are usually associated with concentrations of prey at or near the surface, or within diving range for subsurface foragers. Currently, there are insufficient data on the diets of birds locally and the availability of prey to attempt a detailed explanation of the links between sea temperature and the distribution of seabirds and their prey off southwest Vancouver Island. Euphausiids, however, seem to be a key organism in this regard. *Thysanoessa spinifera* and *Euphausia pacifica* are the common species in this area. Off Vancouver Island, concentrations of euphausiids and other macro-zooplankton are associated with bathymetric breaks, such as the outer shelf-break zone (not sampled in this study), the edges of the larger canyons (especially the inner, northwestern slope of the Juan de Fuca canyon), and over Swiftsure Bank and other midshelf banks (Simard & Mackas 1989, Mackas & Galbraith 1992, Mackas *et al.* 1997). Concentration and advection of euphausiids has been shown to result from upwelling at canyons in this area (Mackas *et al.* 1997, Allen *et al.* 2001). Oblique upward currents carry euphausiids over the shelf edge into areas where they might become accessible to seabirds.

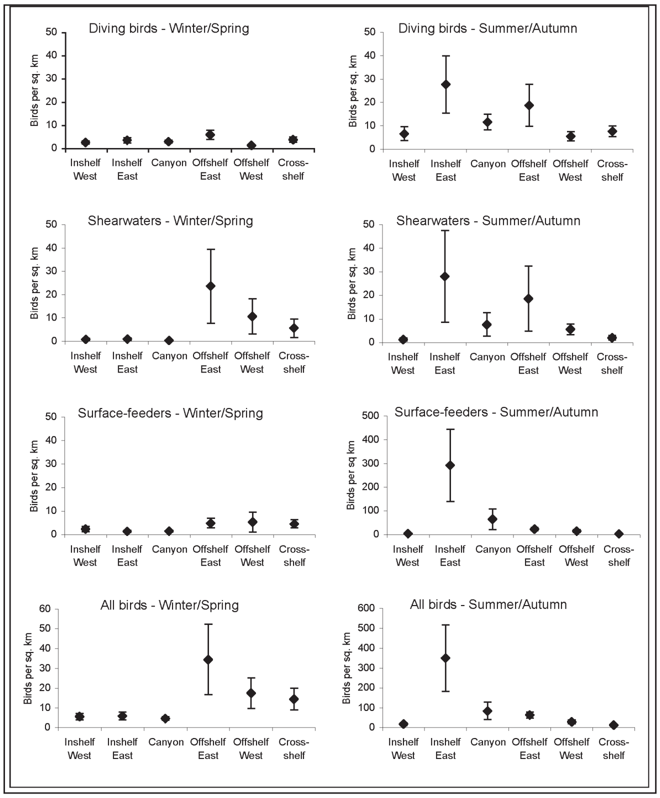

Fig. 5. Mean (± SE) densities of the three major foraging guilds (Divers, Shearwaters, and Surface-feeders) in the six legs of the shelf transects off southwest Vancouver Island in winter/spring and summer/ autumn. Note that the scale of the y-axis varies among the graphs for surface-feeders and all birds; summer/autumn densities were much higher than in winter/spring.

My study confirmed this pattern. The highest prey scores were recorded on the two transect legs immediately adjacent to the canyon. Surface swarms of euphausiids were regularly encountered in summer and autumn during this study, especially on the shelf near Swiftsure Bank and the canyon edge. These swarms were usually accompanied by large flocks of feeding seabirds, including all the common species recorded in the transects. Some larger birds were also seen to take small fish, including herring, which were attracted to the euphausiid swarms.

In contrast to the eddy effects, the cold temperatures generated near the shore by wind-induced upwelling were not associated with advection of euphausiids and other prey species from deeper ocean, and therefore showed lower prey scores and seabird densities. There is a considerable time delay for upwelled nutrients to affect higher trophic levels supporting birds. In my study area Denman *et al.* (1989) concluded that a pulse of primary productivity would take 90 days to create a peak in biomass in euphausiids and fish larvae (food for planktivores) and 270 days in 30 g fish (food for piscivores). By contrast, upwelling and advection of deep canyon water, rich in macro-zooplankton, produces a rapid increase in prey taken by birds as described above.

Seasonal changes in the sea surface temperatures and prey abundance were matched by changes in the densities and distribution of most species of seabirds, involving all the foraging guilds. During winter and spring, temperatures varied relatively little among the six legs, despite a gradual increase of about 4°C from January through June in all legs. Similarly, prey scores and densities of most seabirds showed little variation in density among the six legs in these seasons, with no statistically significant differences in any bird species or guild. In contrast, sea temperatures, prey scores and bird densities showed marked differences among the legs during summer and autumn. The two inner legs (Inshelf East and Inshelf West) and the Canyon leg were usually colder than the outer shelf legs and the Cross-shelf leg, likely due to the upwelling processes discussed above. High bird densities were not consistently associated with all the areas of low sea temperature. Bird densities within the Inshelf West leg remained low for most species and all guilds, even though this leg had consistently cold summer/autumn temperatures. Proximity to the Juan de Fuca canyon, in combination with the temperatures, seemed to provide the most optimal conditions for seabirds, within the Inshelf East and Canyon legs. Several species, especially diving birds and shearwaters, showed higher densities in the Offshelf East leg, adjacent to the canyon, even though this leg did not have consistently low SST.

Other factors affecting seabird distributions

Proximity to colonies likely affected some of the distribution patterns seen in this study. Common Murres, Rhinoceros Auklets and Glaucous-winged Gulls breed on Tatoosh Island, about 14 km southeast of the outer portion of the Canyon leg. Parrish *et al.* (1998) reported that proximity to this colony had a strong influence on densities of these three species during the breeding season, and associations with prey concentrations were evident only after controlling for distance from the colony. Proximity to Tatoosh Island might partly explain the high densities of murres and auklets near the canyon edge, although the Canyon leg itself, closest to that colony, did not contain the highest densities. Rhinoceros Auklets, Glaucous-winged Gulls, Cassin's Auklets, and Fork-tailed Storm Petrels nest on Seabird Rocks (Rodway 1991), about 8 km north of Inshelf West leg, but none of these species had high densities within this leg in any season.

Proximity to roost sites on land might partly explain the high densities of gulls within the Inshelf East leg. Many post-breeding California and Glaucous-winged Gulls, which make up the bulk of the summer/autumn flocks, roost on shore each night, and roosting flocks of hundreds to thousands of gulls are a common sight along the adjacent West Coast Trail coastline.

Many species in this study were obviously not affected by proximity to colonies or roost sites, and there were clear seasonal patterns in the abundance of these species, which migrate into the area in spring and summer. Shearwaters, fulmars, kittiwakes, and Sabine's Gulls showed similar distributions to the California Gulls and alcids, but did not breed or come ashore to roost in this area. The concentrations of alcids adjacent to and over the canyon persisted through the autumn, long after all breeding had ceased.

Using sea surface temperatures to monitor seabird concentrations

Several studies have used satellite images of surface temperatures to reliably predict where concentrations of seabirds might occur when associated with meso-scale ocean processes such as eddies, fronts, upwelling plumes and current filaments (Briggs *et al.* 1987, Haney 1989a,b). This study lacked the resources to include satellite imagery as part of the analysis, but clearly that is an important next step for explaining and tracking the distribution of seabirds off southwest Vancouver Island. Predicting the likely distribution of large aggregations of birds using remote sensing has great value in an area where there is a realistic probability of major oil spills.

This study indicates that SST alone is not a reliable indicator of prey abundance or seabird aggregations off southwest Vancouver Island. Although high prey and bird measures were associated with cold water from the Juan de Fuca Eddy in summer and autumn, the cold upwelled water of the inner shelf away from the eddy (Inshelf West) did not show these high measures of prey or birds. Conversely, the outer shelf leg closest to the eddy (Offshelf East) did not consistently show cold SST in summer and autumn, but did have high measures of prey and birds during these seasons. Clearly the interactions of bathymetry, meso-scale ocean currents and physical conditions causing concentrations of zooplankton, fish and seabirds are complex. Heating of stratified surface water might mask the effects of upwelling and enrichment. More detailed analysis of these variables is needed before satellite imagery can be used to reliably predict seabird distributions off southwest Vancouver Island.

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REFERENCES

ALLEN, S. E., VINDEIRINHO, C. THOMSON, R. E. FOREMAN, M. G. G. & MACKAS, D. L. 2001. Physical and biological processes over a submarine canyon during an upwelling event. *Canadian Journal of Fisheries and Aquatic Science* 58:671-684.

BRIGGS, K. T., TYLER, W. B., LEWIS, D. B. & CARLSON, D. R. 1987. Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology* 11:1-74.

BURGER, A. E. 1992. The effects of oil pollution on seabirds off the west coast of Vancouver Island. In: Vermeer, K., Butler R.W. & Morgan K. (Eds.). The ecology, status and conservation of marine and shoreline birds on the west coast of Vancouver Island. Canadian Wildlife Service Occasional Paper No. 75, Ottawa. pp. 120-128

BURGER, A. E. 2001. Diving depths of shearwaters. *Auk* 118: 755-759.

BURGER, A. E. (Ed.) 2002a. Distribution and abundance of seabirds off southwest Vancouver Island. Unpublished report to Nestucca Trust Fund. Available from Ministry of Water, Land and Air Protection, Biodiversity Branch, Victoria, BC.

BURGER, A. E. 2002b. Conservation assessment of Marbled Murrelets in British Columbia: review of the biology, populations, habitat associations, and conservation. Delta, BC: Canadian Wildlife Service, Technical Report Series No. 387.

BURGER, A.E., HITCHCOCK, C.L. & DAVOREN, G.K. In press. Spatial aggregations of seabirds and their prey on the continental shelf off southwest Vancouver Island. Marine Ecology Progress Series

COHEN, P. & AYLESWORTH, R. 1990. Oil spill risk for southern B.C./northern Washington coast marine area. Final report of the States/British Columbia oil spill task force, Appendix VII. Published by Province of British Columbia and the States of Washington, Oregon, Alaska and California.

DENMAN, K.L., FREELAND, H.J. & MACKAS, D.L. 1989. Comparisons of time scales for biomass transfer up the marine food web and coastal transport processes. *Canadian Special Publication on Fisheries and Aquatic Science* 108:255-264.

DENMAN, K. L., MACKAS, D. L., FREELAND, H. J., AUSTIN, M. J. & HILL, S. H. 1981. Persistent upwelling and mesoscale zones of high productivity off the west coast of Vancouver Island, Canada. In: Richards, F. R. (Ed.). Coastal Upwelling. American Geophysical Union, Washington, D.C. pp. 514-521.

FREELAND, H. J. 1992. The physical oceanography of the west coast of Vancouver Island. In: Vermeer, K., Butler R.W., & Morgan K. (Eds.) The ecology, status and conservation of marine and shoreline birds on the west coast of Vancouver Island. Canadian Wildlife Service Occasional Paper No. 75, Ottawa. pp. 10-14.

FREELAND, H. J. & DENMAN, K. L. 1982. A topographically controlled upwelling center off southern Vancouver Island. *Journal of Marine Research* 40:1069-1093.

FORBES, S.T. & NAKKEN, O. (Eds.). 1972. Manual of methods for fisheries resource survey and appraisal. Part 2. The use of acoustic instruments for fish detection and abundance estimation. F.A.O. Manuals in Fisheries Science No. 5. United Nations, Rome.

HANEY, J.C. 1986. Seabird segregation at Gulf Stream frontal eddies. *Marine Ecology Progress Series* 28:279-285.

HANEY, J.C. 1989a. Remote characterization of marine bird habitats with satellite imagery. *Colonial Waterbirds* 12:67-77.

HANEY, J.C. 1989b. Iterative techniques for characterizing marine bird habitats with time-series of satellite images. *Colonial Waterbirds* 12:78-89.

HAY, D. E., HEALEY, M. C., WARE, D. M. & WILIMOVSKY, N. J. 1992. Distribution, abundance and habitat of prey fish on the west coast of Vancouver Island. In: Vermeer, K., Butler R.W., & Morgan K. (Eds.) The ecology, status and conservation of marine and shoreline birds on the west coast of Vancouver Island. Canadian Wildlife Service Occasional Paper No. 75, Ottawa. pp. 22-29.

HAY, R. B. 1992. The oceanic habitats of seabirds: their zonal distribution off Vancouver Island, British Columbia, Canada. *Journal of Biogeography* 19:67-85.

HEALY, M. C., THOMSON, R. E. & MORRIS, J. T. F. 1990. Distribution of commercial troll fisheries off southwest Vancouver Island in relation to fishing success and oceanic water properties and circulation. *Canadian Journal of Fisheries and Aquatic Science* 47:1846-1864.

HUNT, G. L., JR. & SCHNEIDER, D. C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. In: Croxall, J. P. (Ed.) Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge, U.K. pp. 7-41

LOGERWELL, E. A., & HARGREAVES, N. B. 1996. The distribution of sea birds relative to their fish prey off Vancouver Island: opposing results at large and small spatial scales. *Fisheries Oceanography* 5:163-175.

MACKAS, D. L. 1992. Seasonal cycle of zooplankton off southwestern British Columbia: 1979-89. *Canadian Journal of Fisheries and Aquatic Science* 49:903-921.

MACKAS, D. L. & GALBRAITH, M. 1992. Zooplankton on the west coast of Vancouver Island: distribution and availability to marine birds. In: Vermeer, K., Butler R.W., & Morgan K. (Eds.) The ecology, status and conservation of marine and shoreline birds on the west coast of Vancouver Island. Canadian Wildlife Service Occasional Paper No. 75, Ottawa. pp. 15-21.

MACKAS, D. L., KIESER, R., SAUNDERS, M., YELLAND, D. R., BROWN, R. M. & MOORE, D. F. 1997. Aggregation of euphausiids and Pacific hake (*Merluccius productus*) along the outer continental shelf off Vancouver Island. *Canadian Journal of Fisheries and Aquatic Science* 54:2080-2096.

MARTIN, P. W. & MYRES, M. T. 1969. Observations on the distribution and migration of some seabirds off the outer coasts of British Columbia and Washington State, 1946-1949. *Syesis* 2:241-256.

MORGAN, K. H, VERMEER, K. & MCKELVEY, R.W. 1991. Atlas of pelagic birds of Western Canada. Occasional Paper No. 72, Canadian Wildlife Service, Ottawa.

PARRISH, J. K., LEMBERG, N. & SOUTH-ORYSHCHYN, L. 1998. Effects of colony location and nekton abundance on the at-sea distribution of four seabird species. *Fisheries Oceanography* 7:126-135.

PIATT, J. F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. *Studies in Avian Biology* 14:36-51.

PORTER, J. M. & SEALY, S.G. 1981. Dynamics of seabird multispecies feeding flocks: chronology of flocking in Barkley Sound, British Columbia, in 1979. *Colonial Waterbirds* 4:104-113.

RODWAY, M.S. 1991. Status and conservation of breeding seabirds in British Columbia. In: Croxall, J.P. (Ed.) Seabird status and conservation: a supplement. Cambridge, U.K.: ICBP Technical Publication No. 11. pp. 43-102

SCHNEIDER, D. C. 2002. Scaling theory: application to marine ornithology. *Ecosystems* 5:736-748.

SIMARD, Y. & MACKAS, D. L. 1989. Mesoscale aggregations of euphausiid sound scattering layers on the continental shelf of Vancouver Island. *Canadian Journal of Fisheries and Aquatic Science* 46:1238-1249.

THOMAS, A. C. & EMERY, W. J. 1986. Winter hydrography and plankton distribution on the southern British Columbia continental shelf. *Canadian Journal of Fisheries and Aquatic Science* 43:1249-1258.

THOMSON, R. E. 1981. Oceanography of the British Columbia Coast. *Canadian Special Publication of Fisheries and Aquatic Sciences* No. 56, Ottawa.

THOMSON, R. E., HICKEY, B. M. & LEBLOND, P. H. 1989. The Vancouver Island coastal current: fisheries barrier and conduit. In: Beamish, R. J. & McFarlane, G. A. (Eds.). Effects of ocean variability on recruitment and an evaluation of parameters used in stock assessment models. *Canadian Special Publication of Fisheries and Aquatic Sciences* No. 108, Ottawa. pp. 265-296.

VERMEER, K., BUTLER, R. W. & MORGAN, K. H. (Eds.). 1992. The ecology, status, and conservation of marine and shoreline birds on the west coast of Vancouver Island. Occasional Paper No. 75. Canadian Wildlife Service, Ottawa.

VERMEER, K., HAY, R. & RANKIN, L. 1987. Pelagic seabird populations off southwestern Vancouver Island. *Canadian Technical Report on Hydrographic Ocean Science* No. 87. Ottawa.

VERMEER, K., MORGAN, K. H., SMITH, G. E. J. & HAY, R. 1989. Fall distribution of pelagic birds over the shelf off SW Vancouver Island. *Colonial Waterbirds* 12:207-214.

WAHL, T. R., AINLEY, D. G., BENEDICT, A. H. & DEGANGE, A. R. 1989. Associations between seabirds and water-masses in the northern Pacific Ocean in summer. *Marine Biology* 103:1-11.

WAHL, T. R., MORGAN, K. H. & VERMEER, K. 1993. Seabird distribution off British Columbia and Washington. In: Vermeer, K., Butler R.W., & Morgan K. (Eds.) The ecology, status and conservation of marine and shoreline birds on the west coast of Vancouver Island. Canadian Wildlife Service Occasional Paper No. 75, Ottawa. pp. 39-47.

ZAR, J. H. 1996. Biostatistical analysis, 3rd edition. Prentice Hall, Upper Saddle River, NJ.

THE INFLUENCE OF FISH BEHAVIOUR ON SEARCH STRATEGIES OF COMMON MURRES *URIA AALGE* IN THE NORTHWEST ATLANTIC

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SUMMARY

DAVOREN, G.K., MONTEVECCHI, W.A. & ANDERSON, J.T. 2003. The influence of fish behaviour on search strategies of Common Murres *Uria aalge* in the northwest Atlantic. *Marine Ornithology* 31: 123-131.

Although distribution patterns of seabirds at sea have been described for decades, it remains difficult to identify the mechanisms underlying these patterns. For instance, researchers focusing on prey dispersion as the primary determinant of seabird distribution have found high variability in the spatial overlap of bird and prey aggregations, partially due to the scale-dependent nature of such associations. We conducted a study to identify how the behaviour of capelin *Mallotus villosus*, the primary prey species of all vertebrate predators in the Northwest Atlantic, influences the search tactics of Common Murres *Uria aalge* while acting as central-place foragers during chick-rearing. The study was conducted from 1998-2002 on and around Funk Island, the largest colony of murres in eastern Canada (~ 400 000 breeding pairs), situated on the northeast coast of Newfoundland. We made direct measurements of (1) the distribution, abundance and spatial and temporal persistence of capelin aggregations within the foraging range from the colony (~ 100 km) in combination with (2) bio-physical habitat characteristics associated with capelin aggregations, and (3) individual- and population-level arrival and departure behaviour of murres from the colony. During July of 2000, capelin were found to be persistently abundant within specific 2.25 km blocks of transect ("hotspots"). Further study revealed that capelin persisted in hotspots due to bio-physical characteristics suitable for demersal spawning and for staging areas and foraging areas prior to and after spawning. Directions of return and departure flights of murres measured from the colony did not match during the same observation period (~ 1h), indicating that murres departing the colony did not use information on prey distribution provided by the flight paths of flocks returning to the colony (Information Center Hypothesis). Specific commuting routes (regular flight paths) of murres toward and away from capelin hotspots, however, were obvious at sea, and feeding murres consistently marked the location of these hotspots. This provided excellent conditions for murres to locate capelin from memory and by cueing to activities of conspecifics (local enhancement). Hotspots were persistent across years in this region, presumably allowing marine predators to learn the locations of hotspots, resulting in the use of traditional feeding grounds through generations. Hotspots of predators and prey promote energy transfer among trophic levels, a key ecosystem process. Human predators also concentrate fishing activities within these areas and, thus, there is a need to identify hotspots for protection. Persistent hotspots would be particularly amenable to the design of marine protected areas defined by the habitats of marine predators and their prey.

Keywords: foraging, prey dispersion, capelin, *Mallotus villosus*, Common Murre, *Uria aalge*, information centre

INTRODUCTION

In marine ecosystems, focal forage fish species lie at the core of complex food webs, providing essential linkages for energy transfer between zooplankton and upper trophic predators, such as marine birds (Lavigne 1996). Schooling forage fish often form high-density aggregations (Rose & Leggett 1990). Physical characteristics, such as hydrographic regimes, in combination with biological factors, such as food and predator density, influence the distribution and persistence of these aggregations in space and time (Schneider 1991). High densities of forage fish species elicit an aggregative response in marine bird predators (e.g., Cairns & Schneider 1990) and, thus, influence the distributional patterns and foraging strategies of upper trophic consumers in marine systems (e.g., Davoren 2000, Davoren *et al*. 2002). Habitat selection by the dominant forage fish is therefore essential to comprehend the mechanisms underlying distributional patterns of top vertebrate predators and ultimately trophic interactions in marine systems.

Seabirds provisioning offspring on a colony (Central Place Foragers) are physically separated from their foraging grounds (Orians & Pearson 1979). The travel-time between the colony and prey aggregations and the foraging time within these aggregations both limit the rate of food delivery to offspring (Orians & Pearson 1979). To breed successfully, central place foragers must be proficient at locating food. The Central-Place Foraging model (Orians & Pearson 1979) predicts that colonial animals minimize the duration of round trips and, thus, seabirds likely employ tactics that minimize the time spent searching and capturing prey. An example of this is seabirds using past experience (e.g., Irons 1998). Individuals also can reduce the time spent searching by using information provided by other conspecifics (Wittenberger & Hunt 1985). The Information Center Hypothesis (ICH) postulates that information about the location of prey aggregations beyond the visual range of the colony is exchanged among individuals at the colony (Ward & Zahavi 1973). For instance, naïve birds may follow "successful" ones to prey aggregations (Ward & Zahavi 1973) or track the routes of successful birds returning to the central place from foraging grounds (Gaston & Nettleship 1981; Burger 1997). Information also can be exchanged by cueing to the foraging activities of others within sight, a process known as local enhancement (Wittenberger & Hunt 1985). The degree to which these different strategies are used by seabirds depends on the persistence of prey aggregations in time and space.

The Common Murre *Uria aalge* is a pursuit-diving marine bird that dives to depths up to 200 m (Piatt & Nettleship 1985). Their wing design compromises aerial (high surface area) and underwater flight (low surface area; Thompson *et al*. 1998) and results in high wing-loading (i.e. body mass to wing area ratio: 2.06 g cm^{-2}; Guillemette 1994). Therefore, energy expenditure is elevated during flight compared to most other seabirds. Murres are highly colonial and lay a single egg clutch. The chick is reared at the colony by both parents for 3 weeks. One parent remains at the colony with the chick while the other is on a foraging trip. After most foraging trips, the parent delivers a single fish to its chick. Prior to departure on a foraging trip, murres commonly land on the water in close proximity to the colony (splashdown area, Burger 1997). Murres also regularly return to the colony in large flocks (Gaston & Nettleship 1981, Burger 1997), which presumably indicates the direction of travel from foraging grounds. It has been suggested that these flocks provide the potential for murres in the splashdown area to use an ICH-type mechanism to determine the location of foraging areas beyond visual range of the colony (Gaston & Nettleship 1981, Burger 1997).

In Newfoundland, murres feed their chicks and themselves primarily female capelin *Mallotus villosus* (Müller, 1776) during the breeding season (Davoren & Montevecchi 2003). Capelin, a small, short-lived, pelagic fish, is the main prey of marine birds, mammals and piscivorous fish (Carscadden *et al*. 2002). Capelin migrate into coastal waters from the shelf edge during spring to spawn (Templeman 1948). At this time, capelin schools can be patchily distributed and ephemeral at small spatial scales (1-1000 m) but can also be predictably located within larger regions (1-100 km) in different seasons (e.g. Methven & Piatt 1991). Different stocks have varying spawning habitat preferences, with capelin stocks in Newfoundland primarily considered to spawn on or immediately adjacent to beaches (Templemen 1948), whereas stocks elsewhere in the world primarily spawn off-beach or demersally (Vilhjalmsson 1994). Spawning site characteristics vary, including sediment size range (0.1 - 25 mm), water depth (0 - 100 m) and water temperature (0 - 12ºC; Vilhjalmsson 1994).

We conducted a study to identify how the behaviour, particularly habitat utilization, of forage fish shapes the search tactics of central-place foraging seabirds. Due to the energetically costly nature of search activities for murres, we hypothesize that they will minimize search efforts. During July 2000, we directly measured the distribution and spatial and temporal persistence of capelin within the foraging range of murres from Funk Island, the largest colony of murres in eastern Canada, situated on the northeast coast of Newfoundland. During July-August 2001-2002, we described the bio-physical habitat characteristics that were associated with high-abundance aggregations of capelin. During July-August 1998-2000, we quantified individual- and population-level arrival and departure behaviour of provisioning murres from Funk Island within and among days. We combined this information to infer the relative use of information exchange and past experience, in locating capelin from the colony.

METHODS

Study area

This study was conducted during 1998 - 2002 on and around Funk Island (49°45'N, 53°11'W) on the east coast of Newfoundland (Fig. 1). Funk Island lies 60 km from the coast and supports a common murre population of 340 000 - 400 000 breeding pairs (Birkhead & Nettleship 1980). Throughout this study, murres delivered primarily capelin to their chicks (94% by number, Davoren & Montevecchi 2003), which is consistent with long-term dietary trends throughout Newfoundland (e.g., Burger & Piatt 1990).

Survey design

During July 2000, an 800 km survey was conducted to the southwest of Funk Island aboard the 23 m Canadian Coast Guard Vessel *Shamook*. The location of the survey track was based on observations of flight directions of murres in 1997, observations of high-abundance capelin-murre aggregations enroute to Funk Island from 1977 - 1997 (WAM unpubl. data) and the location of traditional cod and capelin fishing areas (L. Easton, pers. comm.). The survey consisted of nine east-west (across shelf) hydroacoustic transects at a 5 Nm (9 km) north - south spacing. Two east-west transects were conducted during each 12 h day. Seabirds were counted continuously during acoustic transects. The survey was periodically interrupted to sample acoustic signals using a modified shrimp trawl. This survey was conducted once over 5 days, followed by a 2 week period when shorter (2.25 km) transects were repeated

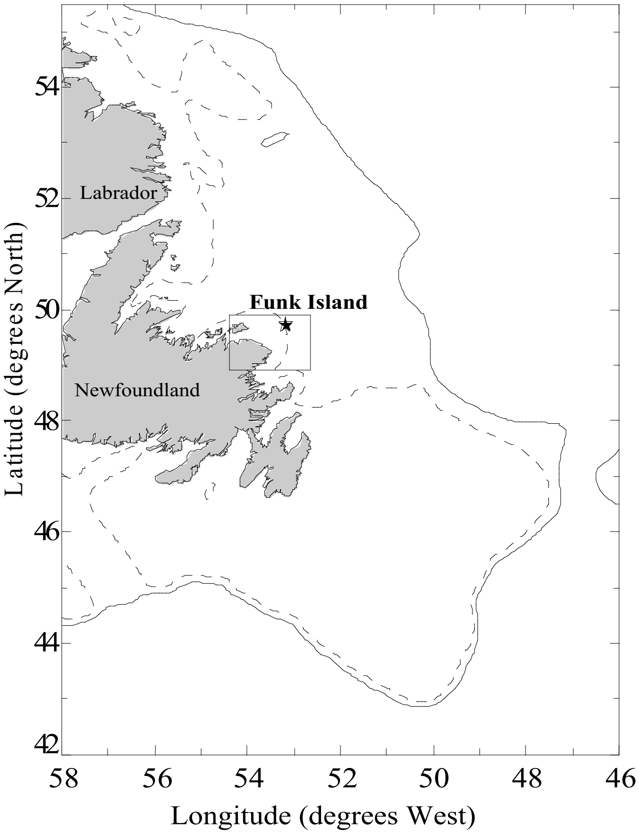

Fig. 1. The map of the study area showing eastern North America's largest colony of Common Murres, the Funk Island Seabird Ecological Reserve. Depth contours are 200 m (– – –) and 500 m (———) and the study area is indicated (rectangle).

along the initial survey track in areas of high capelin abundance. During these shorter transects, acoustic estimates were conducted simultaneously with seabird counts, as in the initial survey.

Acoustic estimates

The relative abundance and distribution of capelin was quantified using a Simrad EQ100 echosounding system, operated through a hull-mounted single-beam transducer with a frequency of 38 kHz. This frequency is appropriate for observations of fish targets and the distinct shape of capelin schools allows them to be separated from other fish species (e.g., American sandlance *Ammodytes americanus*, Atlantic herring *Clupea harengus*) within the study area (O'Driscoll *et al*. 2000). The transducer had a 10-degree beam angle and the echosounder was operated at 1 ping per s, a range of 150 m at one-tenth power, and a bandwidth of 0.3 ms. The transducer was at a depth of 3 m and beam pattern did not form within a range of 5 m; therefore, acoustic signals were not reliable until 8 m. The sample depth of the acoustic system (8 - 250 m) and boat speed (14-16 km h^{-1}) were held constant throughout the July 2000 survey, as were all other echosounder settings. Echograms were continuously printed during transects and latitude and longitude were recorded every 10 min. Following Piatt (1990), the relative abundance of capelin was quantified by estimating the percent cover of the prey backscatter trace in each 1 min (250 m) by 10 m vertical bin on the echogram. Percent cover of prey was estimated on a scale of 0 - 9 in each bin (acoustic abundance score) and this figure was squared before analysis to attain a better estimate of relative abundance (Piatt 1990).

The species composition of acoustic signals was ground-truthed by deploying a modified shrimp trawl. Schools with the greatest uncertainty of acoustic signal were targeted and fishing primarily occurred in areas where many schools were observed. The trawl was used to fish both at the seabed and in mid-water using a standard fishing duration (15 min). The trawl had a 3.5 m headrope and a 12 m footrope, resulting in an opening of 2 m by 8 - 9 m during both bottom and mid-water tows. The mesh size of the body of the trawl was 80 mm and that of the codend was 40 mm. The total mass of the catch and the number of species were recorded immediately after each tow. Ten percent of the catch was sampled and the mass each species contributed to the total catch was calculated. A sample of up to 200 capelin was collected and frozen. In the laboratory, the sex, maturity index (1=immature, 2=maturing, 3=ripe, 4=partially spent, 5=spent) and total length (snout to tip of tail) of each fish were determined. A length stratified sample of two fish per sex per 0.5 cm length category was selected from each sample and the total mass, gonad mass, age and stomach fullness (0%, 25%, 50%, 75%, 100%) of each fish were recorded.

Seabird counts

Seabird densities were estimated during acoustic surveys using standardized strip transect methods (Method I b, Tasker *et al*. 1984) during daylight hours. One observer made continuous counts from the bridge (~3 m above sea level) using binoculars out to 300 m in a 90° arc from the tip of the bow to the port side of the ship. Counting was discontinued if visibility was < 300 m (e.g., fog, high wind). Counts and behaviour (sitting on the water, feeding, flying and flight direction) of birds were entered directly into a laptop computer. The laptop was interfaced with the navigational system of the vessel and counting software (D. Senciall, Birds & Beasty Counter, 1998, Fisheries and Oceans Canada, version 1.0) was used to append a position (latitude and longitude) to each entry. In subsequent analyses, we use murres that were flying, sitting and feeding.

Definition of hotspots

The survey was divided into a continuous series of 250 m horizontal bins, the minimum distance recognizable on the echogram. The squared acoustic abundance scores (scale: 0-81) were summed over the water column for each 250 m bin and then the mean squared abundance scores per 2.25 km block were calculated by averaging these 250 m depth integrated scores. The 2.25 km block is based on the estimate that birds on the water could visually cue to the activities of others within a distance of 4.5 km (Haney *et al*. 1992). These blocks with above average squared acoustic abundance scores were considered to be high-abundance capelin blocks. These high-abundance blocks were revisited on at least 2 occasions over a two-week period after the initial 5-day survey in July 2000, during which a 2.25 km long acoustic transect was conducted simultaneously with seabird counts along the initial survey route. The persistent presence of acoustic prey and murres within high-abundance capelin blocks was quantified by dividing the number of times each 2.25 km block contained capelin and murres by the number of times this block was visited (initial survey and revisit transects). These blocks were revisited over a two week period and, thus, this is the temporal scale of persistence. The mean squared acoustic abundance score ± S.E. was also calculated in each 2.25 km high-abundance block over all visits (maximum: n=4). The 2.25 km blocks where capelin was persistently present were defined as "hotspots".

Bio-physical habitat characteristics of hotspots

During July of 2000, we characterized the bio-physical factors within three persistent hotspots to describe habitat characters associated with persistence. Temperature profiles of the water column were measured using a SeaBird SBE-25. Devices were deployed at 1 m s^{-1}, allowing data capture every 20 - 50 cm from the ocean floor to the surface. Zooplankton biomass was measured by towing a 0.232 mm *Nitex* mesh bongo net, with a 0.29 m^2 mouth opening, at an average speed of 0.88 ± 0.15 m s^{-1} S.E. vertically upwards from the seabed to the ocean's surface. Nets were washed thoroughly into a 1 L sample jar and preserved in a 5% formalin-seawater solution. Half of the sample was oven-dried at 75ºC for 48 h and then weighed to the nearest 0.001 g. Zooplankton biomass per area of water sampled (g m^{-2}) was calculated, based on the volume of water filtered and the depth range sampled.

During July 2001, we returned to each of the three hotspots to characterize the particle size range of the seabed using a 0.3 m^2 Van Veen Benthic Grab System. A 250 ml sample was preserved in a 10% buffered formalin-seawater solution. Samples were later soaked in a 2% KOH solution for 24 h to detach biological material (e.g., fish eggs) adhered to sediment particles. Biological matter was preserved in a 5% formalin-seawater solution and remaining sediments were oven-dried at 75ºC for 48 h. Sediments were poured over a series of 12 graded sieves (0.15 - 31.5 mm), according to the Udden-Wentworth scale of sediment size classification (Wentworth 1922). Size fractions were weighed to the nearest 0.001 g. During August 2002, we again returned to these three hotspots with a Remote Operated Vehicle (ROV) equipped with an underwater video camera (VideoRay Pro) with the main goal to observe and describe capelin schooling behaviour within these persistent areas.

Colony-based departure/arrival behaviour of murres

Population-level return behaviour of murres to Funk Island was observed from 1998 - 2000. Observations were conducted from the highest point on land and each 45° sector was scanned for 1 min using compass-equipped binoculars (7 x 50) with the horizon in the mid-line of view. The number of birds returning during 1 min in each sector was recorded. Three 360° rotations were conducted and defined as a 360° scan, lasting a total of 24 min. Before and after each 360° scan, weather variables (visibility, precipitation, wind speed (km h^{-1}), using a hand-held anemometer, and direction) were recorded. Murres departing Funk Island initially landed on the water in vicinity of the colony (splashdown area), as at other colonies (Burger 1997). Individual-level departure behaviour of murres was observed immediately after each 360° scan in 1999 and 2000. The same site was always used for return and departure observations to minimize biases in the subjective determination of flight directions and to maximize the accuracy of flight directions. We chose 10 individuals leaving different regions of the splashdown area and recorded the final bearing of departure (departure scan). Zigzag flight was observed within the first min but flight direction generally stabilized before the bird was lost from view. The 360° and departure scans together were defined as a sample period, lasting approximately 1 h.

Sample periods were conducted 4 times per day, weather permitting. The 16 h of daylight (0530-2130) was broken into four 4 h intervals (0530-0930, 0930-1330, 1330-1730, 1730-2130 h) and a sample period was conducted in each interval. Sample periods that were separated by ~4 h were considered to be consecutive samples during later analysis. Weather data were used to eliminate sample periods when visibility was compromised. The total numbers of birds returning to the colony during each 360° scan and departing the colony in each departure scan was calculated for each 45° sector. The mean and modal angles of return and departure were calculated following Batschelet (1981). A Rayleigh Test was conducted on each 360° scan and each departure scan to determine if birds returned to or departed the colony in random directions within one sample period (Batschelet 1981). Circular correlations were computed for the mean return and departure angles during consecutive sample periods (separated by 4 h) to determine if successive return directions and departure directions, respectively, were similar (Zar 1996). The mean angle of departure was also compared with the mean angle of return in the same sample period using circular correlations. The results of these analyses are reported as the upper and lower circular correlation coefficients and are deemed not significant at $\alpha=0.05$ if these coefficients span zero (Zar 1996).

RESULTS

Distribution patterns of capelin and murres

During the survey in 2000, the majority of the fish collected with the trawl on 17 occasions were capelin (96% by mass; Davoren 2001) and, thus, we assume that most acoustic signals came from capelin. Capelin schools were present in 41% of the 2.25 km blocks (n=353). Five percent of these blocks had above average acoustic abundance scores (0.8 ± 0.1) (Fig. 2a). Blocks with above average capelin abundance were concentrated within three areas (Fig. 2b), each having distinct water depth characteristics. In areas 1 and 3, blocks were in deep water trenches (> 100 m), whereas blocks were in shallow slope water (< 50 m) in Area 2. In areas 1 and 3, capelin were 100% persistent in each 2.25 km block, or were always present and, thus, were defined as "hotspots" (Area 1: 1, 2; Area 3: 14; Table 1, Fig. 2b). Capelin abundance in these three hotspots remained above average among visits (Table 1). In Area 2, 11 high-abundance capelin blocks were present (3 - 13), four of which had 100% persistence of capelin (3, 7, 11, 13), but seven of which had less consistent presence of capelin (Fig. 2b; Table 1). Capelin abundance in these 2.25 km blocks in Area 2 varied among visits and was not consistently above average (Table 1).

Sitting and flying murres were always present, within all three areas where capelin hotspots were documented, but bird abundances varied widely among visits (Table 1; Fig. 3). Consistent flight paths, or commuting routes (Schneider *et al.* 1990), between these three areas and Funk Island were observed at sea along a northeast-southwest line (Fig. 3a). There also appeared to be movement of birds among these areas, evidenced by northwest-southeast flight trajectories (Fig. 3b). Overall, both sitting and flying murres constantly marked the location of hotspots at sea. For a more detailed examination of the distributional patterns and spatial overlap of murres and capelin during this study see Davoren *et al.* (2003).

Bio-physical habitat characteristics

Capelin schools within areas 1 and 3 were associated with the seabed and occupied distinct deep-water depressions or trenches (100 - 180 m). Three capelin schools were sampled via the bottom-

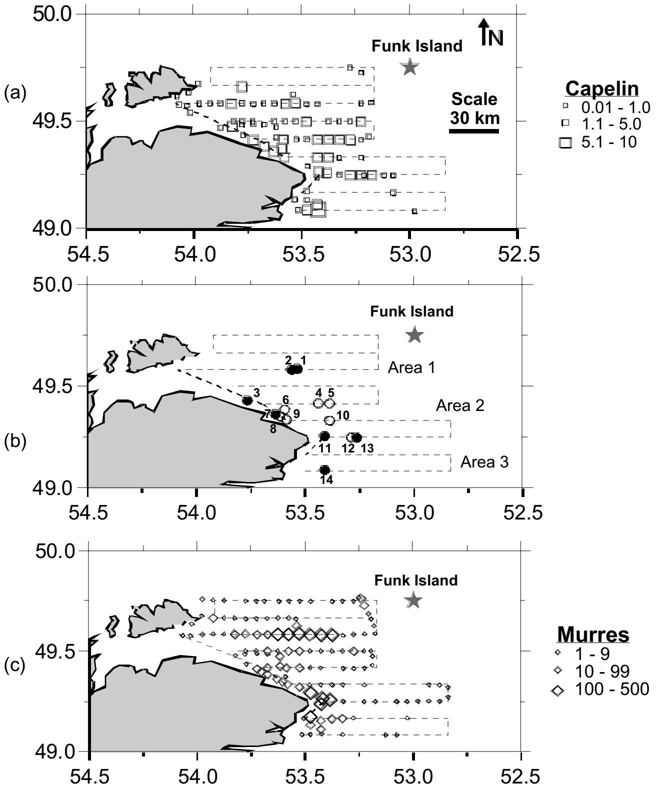

Fig. 2. The distribution of (a) capelin in 2.25 km blocks around Funk Island, (b) high-abundance 2.25 km blocks of capelin, indicating whether capelin were 100% persistent (solid circles) or whether capelin were < 100% persistent (open circles) in space and time, and (c) sitting Common Murres around Funk Island in 2.25 km blocks during the July 2000 survey. Note that hotspots 1, 7, and 14 were those that were revisited for bio-physical habitat characterization.

TABLE 1

The persistence and mean relative abundance of capelin (*Mallotus villosus*) and common murres (*Uria aalge*) ± SD per 2.25 km transect block with above average capelin abundance scores, that were visited around Funk Island in 2000 along with zooplankton densities and temperature profiles of the water column in three hotspots.

	Capelin		**Murre**		**Zooplankton**	**Temperature**					
2.25 km Block No.	No. Visits	Mean Abundance/ 2.25 km	No. Visits	Mean Abundance/ 2.25 km	Density (g m^{-2})	0 m	10 m	25 m	50 m	75 m	100 m
Area 1											
1	3*	1.21 ± 0.31	3	17.59 ± 13.00	4.6 ± 0.5 (2)**	13.2 ± 0.1 (5)	10.2 ± 0.4 (5)	3.0 ± 0.3 (5)	0.3 ± 0.1 (5)	-0.6 ± 0.1 (4)	-0.9 ± 0.1(3)
2	4*	1.05 ± 0.22	4	3.03 ± 2.39							
Area 2											
3	3*	0.80 ± 0.63	3	1.00 ± 0.88							
4	4	1.02 ± 0.79	4	2.07 ± 1.34							
5	4	0.51 ± 0.50	3	0.29 ± 0.26							
6	4	0.26 ± 0.25									
7	3*	1.02 ± 0.90	3	0.98 ± 0.91	1.4 ± 0.6 (2)	13.9± 0.1 (4)	10.6 ± 1.5 (4)	3.1 ± 0.6 (4)	0.4 ± 0.1 (3)	-	-
8	3	0.85 ± 0.78	3	2.78 ± 2.47							
9	4	0.56 ± 0.47	4	2.96 ± 2.91							
10	3	0.37 ± 0.32	4	2.71 ± 1.74							
11	4*	0.25 ± 0.24	3	2.85 ± 2.52							
12	3	0.65 ± 0.59	3	1.01 ± 0.87							
13	3*	0.86 ± 0.76									
Area 3											
14	3*	5.90 ± 2.58	4	1.00 ± 0.78	5.4 (1)	11.4 (1)	6.8 (1)	1.1 (1)	0.1 (1)	-0.4 (1)	-0.8 (1)

* Indicates the individual 2.25 km blocks where capelin were persistently present, calculated as the number of visits (initial survey and other visits) with capelin present divided by the total number of visits, and which were defined as "hotspots".

** Number in parentheses is the sample size.

trawl in Area 1. Schools were composed of near equal ratios of male and female capelin (49-64% females) and males were primarily maturing (maturing: 36-52%; spent: 0-2%; immature: 0%) as were females (maturing: 40-51%; spent: 9-15%; immature: 0%). The majority (~ 90%) of these fish also had < 50% of their stomachs full. In contrast, schools in Area 3 (n=2) were composed of female capelin (89-99%) and males were primarily immature (maturing: 0-2%; spent: 0-2%; immature: 0-10%) whereas females were primarily spent (maturing: 2-5%; spent: 76-97%; immature: 0-8%). The majority (~ 90%) these fish had > 50% of their stomachs full. In contrast, capelin schools within Area 2 were found over shallow slope water (< 50 m) and were off the seabed. These schools (n=5) were composed primarily of female capelin (92-100%), having both spent and mature females (maturing: 7-65%; spent: 30-100%; immature: 0%) with some males (maturing: 0-8%; spent: 0%; immature: 0-2%). Approximately 50% of these fish had their full stomachs.

Zooplankton biomass was similar in areas 1 and 3, but was lower in Area 2 (Table 1). The temperature profiles of the water column at hotspots in the three areas were highly stratified, with similar thermocline depths (25-50 m). There was no evidence of frontal structure or areas where the water column was well-mixed (Davoren 2001). In Area 2, water temperature remained > 0°C at all depths, indicating that capelin schools were exposed to warmer water relative to Areas 1 and 3, where capelin schools were associated with the seabed and occupied < 0°C water temperature (Table 1). Sediment samples in Area 1 (n=3) primarily consisted of silt and fine sand (68%), with smaller percentages (~ 10%) each made up of coarse sand, pebble and cobble. Samples in Area 3 (n=2) primarily consisted of silt and fine sand (99%), with no pebble or cobble and a small percentage of coarse sand (1%). Sediment samples in Area 2 (n=3) had a variety of different types, one with primarily pebble (76%), one with mostly silt and fine sand (96%), and one with half fine sand and silt and half cobble. In August 2002, high densities of fertilized capelin eggs were found adhered to sediments at two sites within one hotspot in Area 2 (hotspot # 11), using the ROV. The spawning sites were located at similar water depths (range: 27-34 m) over flat ground consisting of either coarse sand (<1 mm) or pebble (2-4 mm). The water temperature at the seabed (range: 2.9 - 9.2°C) was similar at both sites.

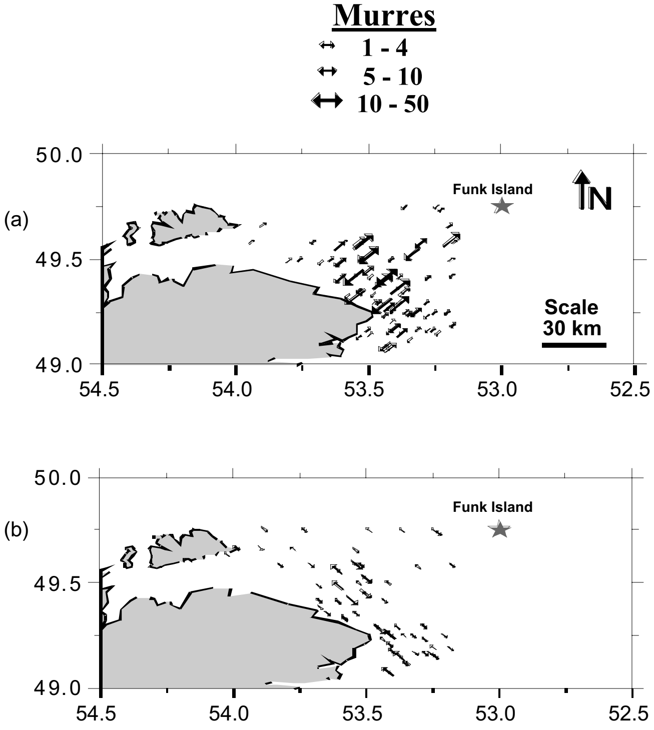

Fig. 3. The distributions and abundances of Common Murres flying in (a) northeast and southwest, and (b) northwest and southeast in 2.25 km bins around Funk Island during the July 2000 survey.

Arrival and departure behaviour of murres

Eighty-eight 360° scans were conducted during 29 d (1998: 11 d, 1999: 10 d; 2000: 8 d) on Funk Island (range: 1 - 6/d). The total number of individuals observed during a scan ranged from 228 - 6060. The modal direction of return, from the south-southwest (180° - 270°), was consistent among years of this study (1998 - 2000) and, thus, years were pooled. Birds generally returned to the colony from all eight sectors during each 360° scan; however, return directions were always nonrandom. Return directions were positively correlated with those in sample periods that were 4 h apart throughout a day (lower CI = 0.5860, upper CI = 0.5978, n= 57, $P < 0.05$; Fig. 4a), indicating similar return directions within days.

Thirty-six departure scans were conducted at Funk Island. The number of individuals observed ranged from 8-13, for a total of 293 individuals. The modal direction of departure was toward the west-southwest (225° - 270°) and was consistent among years (1999-2000) and, thus, years were pooled. Departure directions of murres were significantly nonrandom in 53% of the departure scans. Departure directions were negatively correlated with those in sample periods 4 h apart throughout a day (lower CI= -0.0872, upper CI = -0.0540, n=20, $P < 0.05$; Fig. 4b), also indicating variable departure directions of individuals within days. The majority of birds departed the colony alone (81%, n=239) and the remaining 19% left in flocks of 2 - 13 individuals (mean: 4.4 ± 0.3; median: 4; mode: 2). Return directions were negatively correlated with departure directions during the same sample period (lower CI = -0.1120, upper CI = -0.0937, n=35, $P < 0.05$; Fig. 4c), indicating dissimilar return and departure directions on a temporal scale of 1 h. Unlike other studies, coordinated feeding flocks (Hoffman *et al.* 1981) were never observed in the study area. It is also important to note that flight directions were variable and inconsistently related to wind direction and speed (see Davoren *et al.* 2003).

DISCUSSION

Capelin were persistent over a scale of two weeks within the foraging ranges of murres from Funk Island. Capelin hotspots were persistent likely due to the use of suitable habitat for spawning (Area 2), as well as deep-water depressions or trenches (> 100 m) as staging areas prior to spawning (Area 1) and as recovery areas after spawning (Area 3). Because the location of capelin was persistent, murres could have used previous experience to relocate them. This would explain why murres did not appear to use information on the direction of foraging grounds from the flight trajectories of flocks returning to the colony. Flying (commuting routes) and sitting murres consistently marked capelin hotspots, also providing opportunities for birds to locate capelin by cueing on the foraging activities of conspecifics (local enhancement; Wittenberger & Hunt 1985). Overall, the persistence of capelin hotspots due to specific habitat requirements appeared to influence the distribution patterns and foraging strategies of murres.

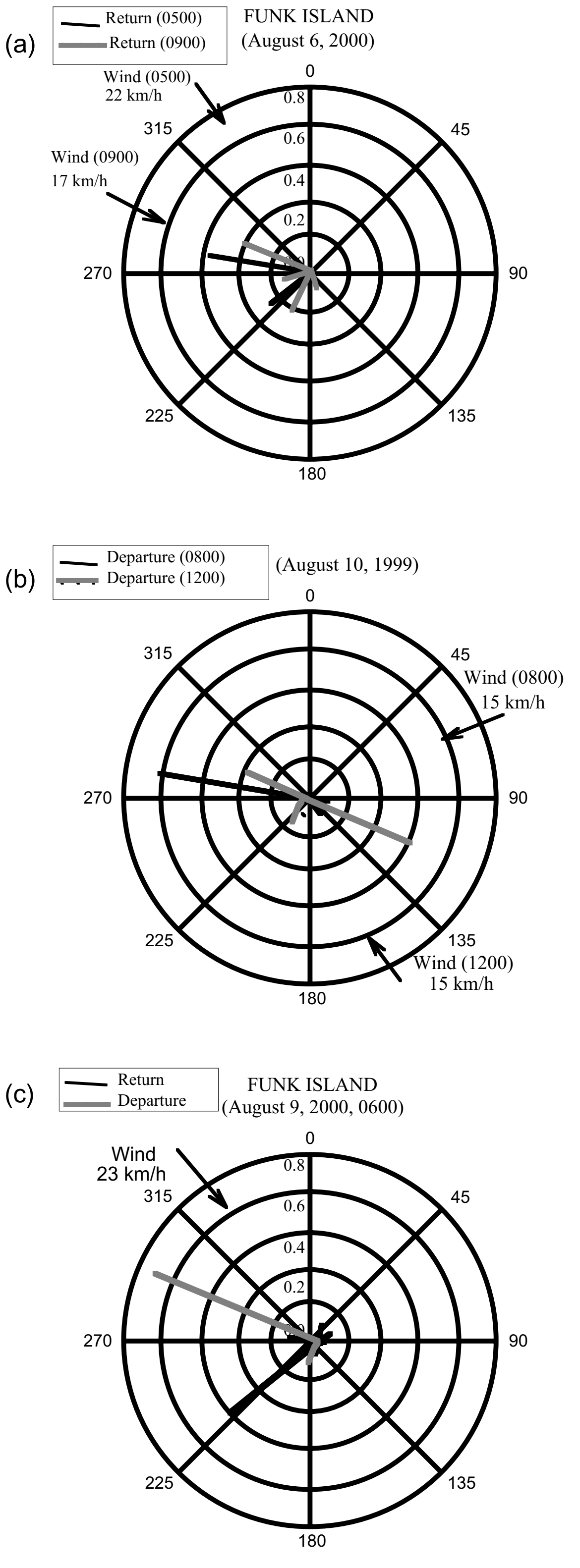

Fig. 4. Circular plots of the proportions of Common Murres returning to and departing from Funk Island in 45º sectors on three representative days, illustrating: (a) returning flight directions in successive sample periods, (b) departure flight directions from the splashdown area in successive sample periods, and (c) return and departure flight directions from the splashdown area in the same sample period. Dotted and solid lines are offset within each 45º sector for clarity.

Why were capelin hotspots persistent?
The presence of maturing capelin in Area 1 and spent capelin in Areas 3 suggests that these are staging areas prior to and after spawning, respectively. Schools in Area 1 comprised primarily maturing capelin with < 50% of their stomachs full, suggesting that feeding was not a priority for these fish. Previous studies have shown that prior to spawning, feeding rates decrease (Vesin *et al.* 1981). In contrast, the majority of spent capelin had > 50% of their stomachs full. Spent capelin begin actively feeding after spawning, increasing their fat content by 20% before the onset of winter (Vesin *et al.* 1981). The occupation of deep water, where zooplankton biomass is higher (GKD unpubl. data) and water temperatures are colder, may allow feeding and maintenance of low metabolic demands, thereby promoting recovery from spawning or gondal development. Occupying deep water also may allow predator avoidance. For fish in both areas 1 and 3, occupying depths of > 100 m is likely ineffective to escape the majority of the diving predators in the study area, but may reduce the risk of predation due to lower illumination at these depths, as well as the time available for prey location and capture by air-breathing predators. In addition, Atlantic cod generally occupy temperatures between - 0.5 to 8.5ºC (Rose & Leggett 1990) and capelin schools in area 1 and 3 were generally found in < - 0.8°C. Although few cod were observed in the study area (GKD unpubl. data), this species was the dominant capelin predator prior to the stock collapse in the early 1990s (Walters & Maguire 1996). Therefore, these habitat features may reflect previously important thermal refuges for avoiding predation by cod (Rose & Leggett 1990). Finally, the two sites found within one capelin hotspot in Area 2 were previously undescribed demersal spawning sites. The presence of suitable physical habitat characteristics for spawning, primarily particle size composition of the seabed and temperature, resulted in the persistent aggregation of capelin among years of this study.

How did capelin hotspots influence search strategies of murres?
Reducing the time spent searching for prey is important during breeding when time constraints and energetic demands are high (Cairns *et al.* 1990). We found no support for the use of directional information provided by large flocks of murres returning to colonies to locate foraging habitats beyond visual range of the colony. Using this Information Center mechanism at the colony represents a poor search tactic because the return trajectories reflect general directions of the last foraging site and are influenced by varying wind conditions (i.e., speed, direction; Burger 1997). We hypothesize that this tactic provides the least accurate information on foraging ground locations. Alternately, search effort could be minimized to a greater degree if the location of persistent food aggregations could be retained in memory. Constant streams of birds flying to and from hotspots along specific routes and high densities of murres consistently sitting within capelin hotspots resulted in capelin being marked at sea. Therefore, we hypothesize that a combination of memory and local enhancement is important in locating capelin within the study area, the importance of each likely depending on the resolution of spatial maps and perceptual constraints of murres and other marine predators in general.

One contradictory observation in this study was the inconsistent departure and return directions at the colony but the persistent movement corridors of murres at sea as well as the persistent attendance of capelin hotspots by murres. One explanation is that murres may visit a number of areas on a foraging trip (e.g.,Wanless *et al.* 1990). Evidence for this may be the highly variable abundance of murres at hotspots in this study and others (e.g., Cairns & Schneider 1990) as well as the apparent movement of murres among hotspots (Fig. 3b). Additionally, murres may depart the colony in a general direction (~270°) using memory, but alter their trajectories (226°) as they encounter returning flocks at sea (information exchange). Anecdotal observations of individual murres changing their flight direction in response to a returning flock at sea were observed. This also suggests that local enhancement may be a behavioural mechanism through which movement corridors are formed.

Conclusions

Capelin, the dominant forage fish species in the Northwest Atlantic, formed persistent hotspots, resulting from the use of specific areas as demersal spawning sites and as staging or foraging areas before and after spawning. High densities of capelin elicited an aggregative response in murres, thereby influencing their distribution patterns and foraging strategies. Owing to the reliance of top vertebrate predators on capelin in this ecosystem, persistence of capelin hotspots likely shapes distributional patterns and search strategies of most vertebrate predators. For instance, through their foraging experience in a region, predators could learn the locations of a suite of hotspots. Regular sampling of these sites would allow daily and monthly choice of foraging sites based on recent experience (Schneider, pers. comm.) and could lead to the development and long-term use of traditional feeding grounds through generations (hinterland; Cairns 1989). Major ecosystem-level perturbations could dramatically affect the predictability of key hotspots. A clear example of this is the influence that the collapse of the eastern Canadian ground-fishery has had on the biology and behaviour of capelin (Carscadden & Nakashima 1997). Therefore, these hotspots should be considered key management areas where fishers and researchers work together to minimize the negative interactions among humans and marine organisms (Hooker *et al*. 1999, Hyrenbach *et al*. 2000).

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REFERENCES

BATSCHELET, E. 1981. Circular Statistics in Biology. New York: Academic Press.

BIRKHEAD, T.R. & NETTLESHIP, D.N. 1980. Census methods for murres Uria spp.: a unified approach. Canadian Wildlife Service Occasional Paper, No. 43.

BURGER, A.E. 1997. Arrival and departure behaviour of common murres at colonies: evidence for an information halo? *Colonial Waterbirds* 20: 55-65.

BURGER, A.E. & PIATT, J.F. 1990. Flexible time budgets in breeding common murres: buffers against variable prey abundance. *Studies in Avian Biology* 14: 71-83.

CAIRNS, D.K. & SCHNEIDER, D.C. 1990. Hotspots in cold water: feeding habitat selection by thick-billed murres. *Studies in Avian Biology* 14: 52-60.

CAIRNS, D.K. 1989. The regulation of seabird colony size: a hinterland model. *American Naturalist* 134: 141-146.

CAIRNS, D.K., MONTEVECCHI, W.A., BIRT-FRIESEN, V.L. & MACKO, S.A. 1990. Energy expenditures, activity budgets, and prey harvest of breeding common murres. *Studies in Avian Biology* 14: 84-92.

CARSCADDEN, J.E. & NAKASHIMA, B.S. 1997. Abundance and changes in distribution, biology and behaviour of capelin in response to cooler waters of the 1990s. In: Forage Fishes in Marine Ecosystems. Anchorage: Alaska Sea Grant College Program AK-SG-91-01. pp. 457-468.

CARSCADDEN, J.E., MONTEVECCHI, W.A., DAVOREN, G.K. & NAKASHIMA, B.S. 2002. Trophic relationships among capelin (*Mallotus villosus*) and marine birds in a changing ecosystem. *ICES Journal of Marine Science* 59: 1027-1033.

DAVOREN, G.K. 2000. Foraging variability in response to changing prey distribution in rhinoceros auklets. *Marine Ecology Progress Series* 198: 283-291.

DAVOREN, G.K. 2001. Predator-prey interactions of common murres (*Uria aalge*) and fish in the Northwest Atlantic: foraging strategies on multiple scales. PhD thesis, Memorial University of Newfoundland, St. John's, Newfoundland.

DAVOREN, G.K. & MONTEVECCHI, W.A. 2003. Signals from seabirds indicate changing fish stocks. *Marine Ecology Progress Series* 258: 253-261.

DAVOREN, G.K., MONTEVECCHI, W.A. & ANDERSON, J.T. 2002. Scale-dependent associations of predators and prey: constraints imposed by flightlessness of common murres. *Marine Ecology Progress Series* 245: 259-272.

DAVOREN, G.K., MONTEVECCHI, W.A. & ANDERSON, J.T. 2003. Search strategies of a pursuit-diving marine bird and the stability of prey patches. *Ecological Monographs* 73: 463-481.

GASTON, A.J. & NETTLESHIP, D.N. 1981. The Thick-billed Murres of Prince Leopold Island: A Study of the Breeding Ecology of a Colonial High Arctic Seabird. Canadian Wildlife Service Monograph Series No. 6, Ottawa.

GUILLEMETTE, M. 1994. Digestive-rate constraints in wintering common eiders (*Somateria mollissima*): implications for flying capabilities. *Auk* 111: 900-909

HANEY, J.C., FRISTRUP, K.M. & LEE, D.S. 1992. Geometry of visual recruitment by seabirds to ephemeral foraging flocks. *Ornis Scandinavica* 23: 49-62.

HOFFMAN, W., HEINEMANN, D. & WIENS, J.A. 1981. The ecology of seabird feeding flocks in Alaska. *Auk* 98: 437-456.

HOOKER, S.K., WHITEHEAD, D.H. & GOWANS, S. 1999. Marine protected area design and the spatial and temporal distribution of cetaceans in a submarine canyon. *Conservation Biology* 13: 592-602.

HYRENBACH, K.D., FORNEY, K.A. & DAYTON, P.K. 2000. Marine protected areas and ocean basin management. *Aquatic Conservation* 10: 437-458.

IRONS, D.B. 1998. Foraging area fidelity of individual seabirds in relation to tidal cycles and flock feeding. *Ecology* 79: 647-655.

LAVIGNE, D.M. 1996. Ecological interactions between marine mammals, commercial fisheries and their prey: unraveling the tangled web. In: Montevecchi, W.A. (Ed). High-latitude seabirds. 4. Trophic relationships and energetics of endotherms in cold ocean systems. Ottawa: Canadian Wildlife Service Occasional Paper 91. pp. 59-71.

METHVEN, D.A. & PIATT, J.F. 1991. Seasonal abundance and vertical distribution of capelin (*Mallotus villosus*) in relation to water temperature at a coastal site off eastern Newfoundland. *ICES Journal of Marine Science* 48: 187-193.

O'DRISCOLL, R.L., SCHNEIDER, D.C., ROSE, G.A. & LILLY, G.R. 2000 Potential contact statistics for measuring scale-dependent spatial pattern and association: an example of northern cod (*Gadus morhua*) and capelin (*Mallotus villosus*). *Canadian Journal of Fisheries and Aquatic Sciences* 57: 1355-1368.

ORIANS, G.H. & PEARSON, N.E. 1979. On the theory of central place foraging. In: Horn, D.J., Mitchell, R.D. & Stairs, G.R. (Eds.). Analyses of Ecological Systems. Columbus, Ohio: Ohio State University Press. pp. 154-177.

PIATT, J.F. 1990. The aggregative response of common murres and Atlantic puffins to schools of capelin. *Studies in Avian Biology* 14: 36-51.

PIATT, J.F. & NETTLESHIP, D.N. 1985. Diving depths of four alcids. *Auk* 102: 293-297.

ROSE, G.A. & LEGGETT, W.C. 1990. The importance of scale to predator-prey spatial correlations: an example of Atlantic fishes. *Ecology* 71: 33-43.

SCHNEIDER, D.C., PIEROTTI, R. & THRELFALL, W. 1990. Alcid patchiness and flight direction near a colony in eastern Newfoundland. *Studies in Avian Biology* 14: 23-35.

SCHNEIDER, D.C. 1991. The role of fluid dynamics in the ecology of marine birds. *Oceanography and Marine Biology Annual Review* 29: 487-521.

TASKER, M.L., HOPE JONES, P., DIXON, T. & BLAKE, B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and a suggestion for a standardized approach. *Auk* 101: 567-577.

TEMPLEMAN, W. 1948. The life history of the Capelin (*Mallotus villosus* O.F. Muller) in Newfoundland waters. Bulletin of the Newfoundland Government Laboratory No. 17: 1-151.

THOMPSON, C.W., WILSON, M.L., MELVIN, E.F. & PIERCE, D.J. 1998. An unusual sequence of flight-feather molt in common murres and its evolutionary implications. *Auk* 115: 653-669.

VESIN, J.-P., LEGGETT, W.C. & ABLE, W. 1981. Feeding ecology of capelin (*Mallotus villosus*) in the estuary and western Gulf of St. Lawrence and its multispecies implications. *Canadian Journal of Fisheries and Aquatic Sciences* 38: 257-267.

VILHJALMSSON, H. 1994. The Icelandic Capelin Stock. *Rit Fiskideildar* 8: 1-213.

WALTERS, C.J. & MAGUIRE, J.J. 1996. Lessons for stock assessment from the northern cod collapse. *Reviews in Fish Biology and Fisheries* 6: 125-137.

WANLESS, S., HARRIS, M.P., & MORRIS, J.A. 1990. A comparison of feeding areas used by individual common murres (*Uria aalge*), razorbills (*Alca torda*) and an Atlantic puffin (Fratercula arctica) during the breeding season. *Colonial Waterbirds* 13: 16-24.

WARD, P. & ZAHAVI, A. 1973. The importance of certain assemblages of birds as "information-centres" for food-finding. *Ibis* 115: 517-534.

WENTWORTH, C.R. 1922. A scale of grade and class terms for clastic sediments. *Journal of Geology* 30: 377-392.

WITTENBERGER, J.F. & HUNT, G.L. Jr. 1985. The adaptive significance of coloniality in birds. In: Farner, D.S., King, J.R. & Parkes, K.C. (Ed). Avian Biology. London: Academic Press pp. 1-77.

ZAR J.H. 1996. Biostatistical Analysis. Englewood Cliffs: Prentice-Hall.

CHANGES IN DISTRIBUTION AND ABUNDANCE OF KITTLITZ'S MURRELETS *BRACHYRAMPHUS BREVIROSTRIS* RELATIVE TO GLACIAL RECESSION IN PRINCE WILLIAM SOUND, ALASKA

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SUMMARY

KULETZ, K.J., STEPHENSEN, S.W., IRONS, D.B., LABUNSKI, E.A. & BRENNEMAN, K.M. 2003. Changes in distribution and abundance of Kittlitz's Murrelets *Brachyramphus brevirostris* relative to glacial recession in Prince William Sound, Alaska. *Marine Ornithology* 31:133-140.

The Kittlitz's Murrelet is a diving seabird of relatively low abundance found only in Alaska and eastern Siberia. Prince William Sound (PWS), Alaska, is a population center for this species, where it typically occurs near tidewater glaciers. In PWS, marine bird surveys (n = 7 years) indicated that there was an 84% decline in Kittlitz's Murrelets from approximately 6400 birds in 1989 to 1000 birds in 2000. During this period, the distribution in PWS changed from being fairly dispersed to being concentrated in the northwest region. In 2001 we surveyed for Kittlitz's in PWS, targeting 17 fjords and bays where they had been found in the past or with suitable habitat. We estimated 1,969 ± 1,058 (95% C. I.) Kittlitz's Murrelets in PWS, with 78% of the population in two fjords in the northwest corner, and 20% in three other fjords. With one exception, fjords with > 1% of the estimated population of Kittlitz's Murrelet had advancing or stable glaciers, based on glacial accounts from the late 1980s. The fjords where this species disappeared had receding glaciers as of the late 1980s, or had no direct glacial input. These results are consistent with a link between the decline of Kittlitz's Murrelets and glacial recession. More recent data indicate that several glaciers in the northwest region of PWS are now stagnating or retreating, likely due to global warming (Arendt *et al*. 2002), which in turn might result in further declines in the Kittlitz's Murrelet population. Our findings underscore the importance of tidewater glaciers to Kittlitz's Murrelets, and suggest that pagophilic species are sensitive indicators of climate change.

Keywords: Kittlitz's Murrelet *Brachyramphus brevirostris*, distribution, habitat, population trend, glacial retreat

INTRODUCTION

The Kittlitz's Murrelet *Brachyramphus brevirostris*, a small diving bird in the family Alcidae, may today be the rarest seabird regularly breeding in Alaska. Current population estimates range from 9000-25 000 birds (USFWS 2003). Most of the world population inhabits Alaskan waters, with an estimated 5% of the remaining birds in eastern Siberia (Day *et al*. 1999). Anecdotal accounts of birds at sea and standardized surveys in a few areas suggested that Kittlitz's Murrelets were declining in coastal areas of the northern Gulf of Alaska (GOA) at least since the early 1970s (Kendall & Agler 1998, USFWS 2003). Isleib & Kessel (1973) suggested that the Kittlitz's Murrelet population along the northern GOA was probably a few 100 000s birds, and noted that in several PWS fjords and near the Malaspina-Bering icefields, Kittlitz's 'outnumber all other alcids'; in the 1990s, this was no longer the case (USFWS 2003). By 1998, more complete at-sea surveys derived an estimate of 12 130 ± 8312 (95% C.I.) Kittlitz's for the core population centers in the GOA: Cook Inlet, PWS, and Southeast Alaska (Kendall & Agler 1998). Based on these surveys and scattered records, Day *et al*. (1999) estimated the Kittlitz's world population to be in the 'thousands or very low tens of thousands'.

Small breeding populations of Kittlitz's Murrelet occur along the Aleutian Islands and as far north as the central Chuckchi Sea (Day *et al*. 1999). However, most of the Alaska population appears to have a quite restricted set of habitat preferences, being primarily found near tidewater glaciers or in nearshore waters with glacial runoff (Islieb & Kessel 1973, Day *et al*. 1999, 2003).

Because Kittlitz's Murrelet tend to associate with coastal glaciers, some authors speculated that their apparent decline is related to the retreat of glaciers in Alaska in recent decades (vanVliet 1993, Day *et al*. 1999, 2003). Changes in Alaskan glaciers, while locally dynamic, are generally associated with changes in atmospheric temperatures during the past 100 years (Molnia 2001, Arendt *et al*. 2002). Species with critical parts of their life histories (for Kittlitz's Murrelet, the breeding season) restricted to ice-associated habitats will be the first to respond to climate change (Walther *et al*. 2002, Root *et al*. 2003). However, for Kittlitz's Murrelet, knowledge of the population trends and their linkages to changes in coastal glaciers is very limited.

Our study area, PWS, is a population center for Kittlitz's Murrelet, supporting roughly 15-20% of the known Alaska population (USFWS 2003). Since 1989 the U.S. Fish and Wildlife Service (USFWS) has conducted standardized at-sea surveys in PWS to monitor trends in all species of marine birds (Lance *et al*. 2001, Stephensen *et al*. 2001). These surveys comprise the best existing long-term trend data for Kittlitz's Murrelet. We examined these historical data sets for trends in the PWS Kittlitz's Murrelet population and conducted a vessel-based survey specifically to map the current distribution and abundance of the species. Because Kittlitz's Murrelets tend to associate with coastal glaciers, some authors speculate that the recent and continuing retreat of glaciers in Alaska (Lethcoe 1987, Arendt *et al*. 2002) could be detrimental to the murrelets (van Vliet 1993, Day *et al.* 1999, 2003). Here we present evidence that changes observed in this Kittlitz's population are linked to the status of neighboring glaciers.

METHODS

Study area

All surveys were conducted in PWS, a large embayment in southcentral Alaska with about 9000 km^2 surface water area and over 5000 km of shoreline (Fig. 1). The sound is bordered by the Chugach Mountains, which include several large icefields, each > 800 km^2 which drain into PWS via > 40 fjords and 20 tidewater glaciers (Molnia 2001). The upper portions of fjords with tidewater glaciers are generally only ice free during summer months, and always contain variable amounts of floating brash ice (Molnia 2001, author's pers. obs.). Weather in PWS is characterized by frequent cloud cover and precipitation (Wilson & Overland 1986). Summer air temperatures during 2001 surveys averaged 12°C (range 4-22).

The fjords and bays are diverse in topography and basin depth, ranging from averages of < 50 m deep (usually classified as bays) to > 400 m deep (usually considered fjords) (Gay & Vaughan 1998). Fjords with tidewater glaciers generally have steep-sided basins and underwater sills which may be 4-60 m deep (Gay & Vaughan 1998). Bays, fjords, and large islands without tidewater glaciers typically have non-tidewater glaciers discharging runoff. Throughout PWS, and particularly in the fjords and bays, water is highly stratified during summer, when snow and ice melt peaks. Local hydrographic conditions vary considerably, but compared to average PWS conditions, tidewater fjords tend to have cooler, fresher waters, with stronger, and more shallow (10-15 m) temperature (thermocline) and salinity (halocline) vertical gradients (Gay & Vaughan 1998). Tides are semidiurnal and range up to 6 m.

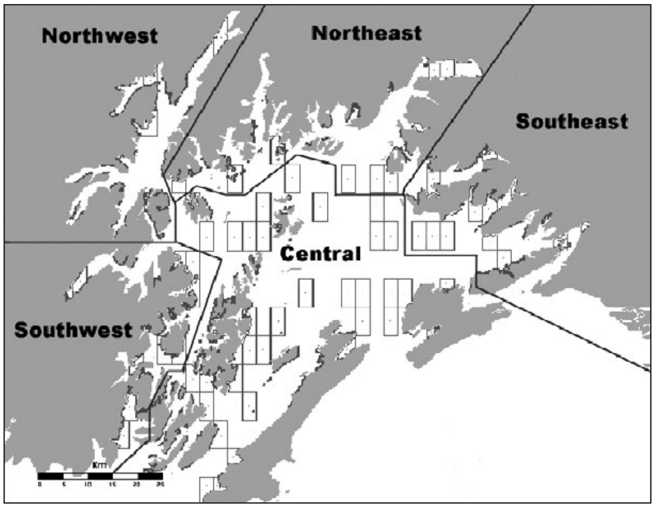

Fig. 1. The Prince William Sound study area for the 1989-2000 sound-wide surveys. Randomly selected shoreline transects (black shoreline) and blocks sampled with pelagic transects are shown within the five regions used to examine spatial population trends.

Data collection

All strip transect surveys were conducted from 8 m fiberglass boats traveling at speeds of 10-20 km hr^{-1}, although observers reduced the cruising speed during sightings to confirm species identification. Two observers recorded all birds < 100 m to either side or ahead of the boat, using binoculars to aid in species identification (Klosiewski & Laing 1994). Most surveys were conducted when wave height was < 0.3 m, and none were done in seas > 0.6 m, to avoid missing birds sitting on the water. The sightings were expressed as an encounter rate (birds km^{-2}).

The USFWS sound-wide surveys were each conducted over ≤ 3 weeks of July in 1989-1991, 1993, 1996, 1998 and 2000. Detailed methods for these surveys were described elsewhere (Klosiewski & Laing 1994, Kendall & Agler 1998). USFWS personnel surveyed 347-351 transects each year except during 1989, when 325 transects were surveyed. Transects were randomly selected from two strata – shoreline (< 200 m from shore), and offshore (> 200 m from shore), with the latter based on two parallel bands within 5' latitude x 5' longitude blocks (Fig. 1). Shoreline transects, defined by geographic features, varied in length (mean = 6.6 km) (Fig. 1). Study design and survey methodology were consistent between 1989 and 2000. During these surveys, Kittlitz's Murrelet abundance estimates had an average coefficient of variation of 0.40 (Nielson *et al*. 2003), which for the sound-wide surveys, results in ~ 65 % probability of detecting a 20 % annual change in population (estimated from Fig. 5, Klosiewski & Laing 1994).

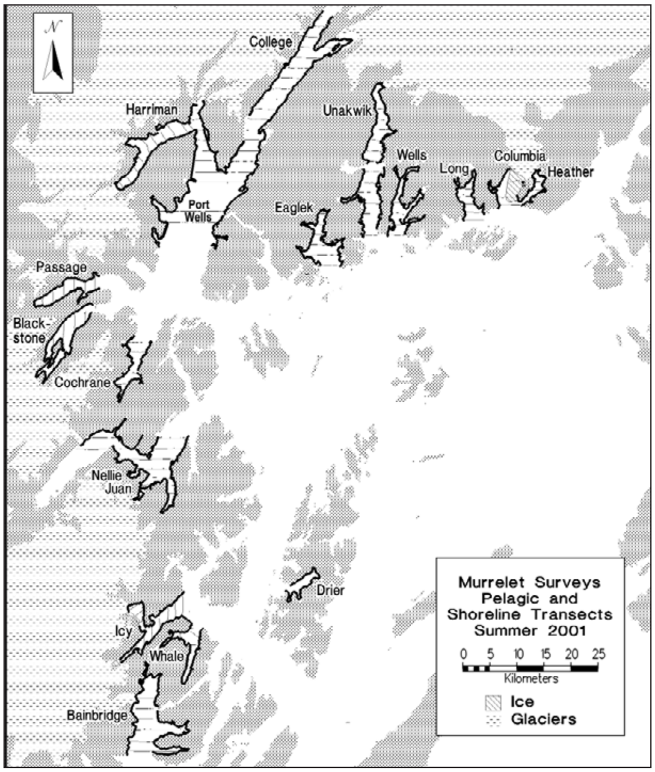

Fig. 2. Surveyed shorelines (black shoreline) and pelagic transects (light, parallel lines) in fjords and bays sampled for the 2001 intensive survey of Prince William Sound.

The sound-wide surveys provided trend data, but did not sample a high proportion of Kittlitz's Murrelet preferred habitat. To solve this problem, we conducted an intensive survey between 22 May and 3 August 2001, targeting 17 fjords and bays in PWS where Kittlitz's have occurred in the past, or that had suitable marine habitat but had not been sampled. Due to time constraints, and because few or no Kittlitz's were observed during sound-wide surveys in the southeastern and central regions since 1993, we did not sample those waters in 2001.

In 2001, we surveyed most of the sites once between late June and late July, during the chick-rearing phase (Day *et al*. 1999). At this time, both members of breeding pairs are at sea and counts of Kittlitz's Murrelet are highest in PWS (Klosiewski & Laing 1994, Day & Nigro 1999, Kuletz *et al*. 2003). Each fjord or bay took 1-2 days to survey, using standard USFWS protocol (Klosiewski & Laing 1994). The intensive surveys included a continuous shoreline count in each fjord and a systematic grid of pelagic transects (> 200 m from shore), which ran roughly perpendicular to shore at approximately 2 km intervals (Fig. 2). We used DLOG software (R.G. Ford Consulting, Portland, OR) to enter observations directly into a computer connected to a global positioning system (GPS), so that every observation was geo-referenced. Four of the fjords were surveyed three times, during the early (22 May-9 June), middle (12-30 June), and late (12 -30 July) summer. For these fjords, we included the survey with the highest Kittlitz's Murrelet density in the final PWS population estimate.

Potential sources of error

Variation in species identification and survey conditions forced us to make assumptions when analyzing the survey and trend data. The two *Brachyramphus* murrelets, the Kittlitz's Murrelet and the Marbled Murrelet *B. marmoratus*, were not always identified to species and the proportion of unidentified birds declined in later years (Stephensen *et al*. 2001). We assumed that the probability of being identified was the same for both species and that identification rates did not vary within a survey. Thus, changes in the abundance of identified Kittlitz's Murrelet were assumed to be representative of changes in the actual population. To investigate the potential confounding effect of higher identification rates in later years we examined population trends of both identified Kittlitz's Murrelets only and total Kittlitz's Murrelets. The latter included the identified birds, plus the portion of unidentified birds that were classified as Kittlitz's, based on the annual percentage of identified murrelets that belonged to that species. For the intensive surveys in 2001, observers were trained to distinguish the two *Brachyramphus* species using photographs, study skins, and on-sight practice prior to surveys. Unidentified murrelets comprised 4% of sightings in 2001, usually due to insufficient viewing time, and they were not combined with identified Kittlitz's Murrelets.

Second, we assumed that changes in ice conditions or weather did not bias counts of Kittlitz's Murrelet over time. All of the sound-wide surveys and most of the intensive survey, occurred from late June through July, when fast ice near glaciers breaks up, brash ice is reduced, and small vessels can maneuver farther into upper fjords (Kuletz *et al*. 2003). Floating ice could have precluded transects in the upper fjords from being surveyed during sound-wide surveys, so we examined the raw data from 1989-2000 for missed transects. Of the 41 transects in upper fjords surveyed over 7 years (*n* = 287), 9 were missed due to ice (3%). Five of the missed transects occurred in 1989, when the Kittlitz's Murrelet population estimate was highest (Stephensen *et al*. 2001). The remaining 4 missed transects contained 1 or 2 Kittlitz's Murrelets sighted in at least one other year. Because of the low proportion of missed transects, most of which occurred the year that Kittlitz's Murrelets were most abundant, we did not revise the population estimates to exclude those transects.

Another possible concern was that observers may have missed birds found in waters hemmed in by ice. Most of the sound-wide surveys did not use GPS, so it was not possible to determine at what point ice might have inhibited our surveys. In 2001, however, the hard-hulled whalers (also used during sound-wide surveys) were able to move into open leads and maneuvered through areas of > 50% and up to 80% ice cover. We rarely sighted Kittlitz's Murrelets in waters with ice cover > 50%, supporting previous findings in the literature (Day & Nigro 2000, Day *et al*. 2003). When the vessel's progress was blocked by ice, the observers scanned open water from the cabin top (~ 4 m above water). Because we did not detect Kittlitz's Murrelets in open leads, we believe that negligible numbers of birds were missed during PWS surveys.

Data analysis

For sound-wide surveys, we estimated the Kittlitz's Murrelet population for each year using the ratio of the total sightings to the area surveyed (Cochran 1977), and the 95% confidence intervals from the sum of the variances of each stratum (Kendall & Agler 1998). The population trend was examined by comparing the log-transformed annual estimates over time. The slope of the regression was tested for a significant deviation from zero, at the alpha 0.05 significance level. The per annum percent change in the population was derived from the back-transformed best-fit slope of the regression.

For the 2001 intensive survey, the population estimate for each fjord was derived from the average density among pelagic transects, extrapolated using the total area of the fjord (for waters > 200 m offshore), plus the total number of birds counted along the shoreline. The total population estimate was then derived by summing the individual estimates for each fjord, and calculating the 95% confidence intervals from the sum of the variances of each fjord. The population estimate for the intensive survey can only be applied to the surveyed areas and is thus a minimum estimate for the entire PWS. However, based on the sound-wide surveys since 1996, these areas encompass 86-90% of the PWS population.

We examined the distribution of Kittlitz's Murrelet over time using the sound-wide surveys, as the same transects were surveyed repeatedly every year. To map bird distributions, we used the total number seen on each transect, and the transect centroid as their location. We divided PWS into five geographically defined regions (Fig. 1). Mainland fjords occurred in the southwest, northwest, northeast, and southeast regions, and large islands and remaining pelagic waters comprised the central region. We summed the number of Kittlitz's Murrelets sighted within each region during a given year, and tested for concordance among regions over time, using Friedman's rank sum test. Due to the low counts (including zeros) in some regions and years, we combined the data into three time periods: 'early' (1989 and 1990), 'middle' (1991 and 1993), and 'late' (1996, 1998 and 2000). We tested the null hypothesis of no association among regions and changes over time at the significance level of alpha = 0.05.

To examine the current distribution of Kittlitz's Murrelet relative to glaciers, we used the intensive survey results, where all sightings was mapped using GPS. We quantified glacier status as advancing, stable, or receding, based on data through the mid-1980s (Lethcoe 1987). We tested for association between Kittlitz's Murrelet occupation of a fjord or bay (occupation was defined as > 1% of the estimated population in 2001) and glacial status of the bay, using Fisher's exact test. We contrasted the number of sites with (n = 5) or without (n = 12) Kittlitz's Murrelet occupation and the number of sites with stable or advancing glaciers (n = 4) vs. sites with retreating or no tidewater glacier (n = 13).

RESULTS

Population trends and abundance

From 1989 to 2000, the population of Kittlitz's Murrelet in PWS declined either 18% (identified only; Fig. 3) or 24% (total) per year. For identified birds, the slope of the regression (r^2 = 0.61) was significantly different from zero (t = -2.79, P = 0.04). The regression for total birds was similar (r^2 = 0.57), and the slope was still significant (t = -2.59, P = 0.05). The population estimate in 2000 was 16% and 10% of the 1989 estimate for identified and for total Kittlitz's Murrelets, respectively.

In 2001, 387 Kittlitz's Murrelets sighted on the water yielded a population estimate for the surveyed fjords of 1969 ± 1058 (95% C.I.) birds. Approximately 98% of the population occurred in five of the 17 fjords, with most (78%) in two adjacent northwest fjords, Harriman and College, with the remainder of the population in Blackstone Bay (6%), Unakwik Inlet (3%), and Icy Bay (11%). Port Nellie Juan, Long Bay, and Heather Bay together contributed only 2% of the total (Fig. 4).

Distribution over time

As the population declined over time, the distribution of Kittlitz's Murrelet in PWS has changed (Fig. 5). In 1989, Kittlitz's Murrelets were most abundant in the northwest and northeast fjords, but occurred throughout PWS, including large numbers in the southeast (Fig. 5; 1989). In 1990 and 1991, low numbers were sighted in the southwest, with most Kittlitz's occurring in the northwest and northeast fjords (Fig. 5; 1990, 1991). In 1993, which was characterized by unusually high numbers of both *Brachyramphus* species (Stephensen *et al*. 2001), there were relatively high numbers of Kittlitz's Murrelet in the central region (Fig. 5; 1993). In 1996 (Fig. 5; 1996), 1998 (which had a distribution similar to 1996 but fewer birds), and 2000 (Fig. 5; 2000), there was a marked absence of Kittlitz's Murrelet throughout most of PWS, except for the northwest region.

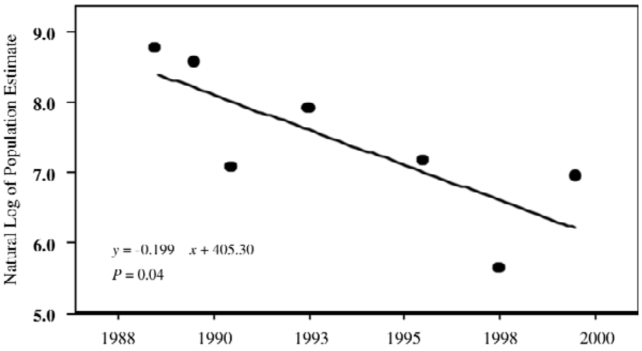

Fig. 3. Population trend of identified Kittlitz's Murrelets in Prince William Sound, based on sound-wide surveys during 1989-2000.

The observed changes in Kittlitz's Murrelet abundance were not synchronous across the five regions we surveyed (Friedman's chi-square = 7.2, df = 4, P = 0.13), suggesting that the onset of the decline varied across the study area. Although all five regions showed a decline between the beginning (1989-90) and the end (1996-2000) of our study, numbers in the southeast remained low after 1989-90, while numbers in the southwest and central regions peaked during the middle period (1991-93) (Fig. 6a). The northwest always had the highest numbers, and supported a greater proportion of the total population over time, comprising up to 55% of the PWS population during the late period (1996-2000) (Fig. 6b). The proportion in the northeast remained stable at about 22% of the total, while the proportions in other regions declined or, following temporarily higher proportions during the middle period, declined in the late period.

Distribution relative to glaciers

In 2001, Kittlitz's Murrelets generally occupied the upper regions of fjords, usually near tidewater glaciers or the outflow from recently grounded glaciers (Fig. 4). Among fjords, their distribution was highly correlated with the status of surrounding glaciers. Substantial numbers (> 1% of the PWS population at a given site) were found at all four sites with stable or advancing glaciers and at only one of the 13 sites with retreating or non-tidewater glaciers (n = 17; Fisher's exact test, P = 0.002). The Harriman and College fjords are surrounded by the greatest number of glaciers (Fig. 4),

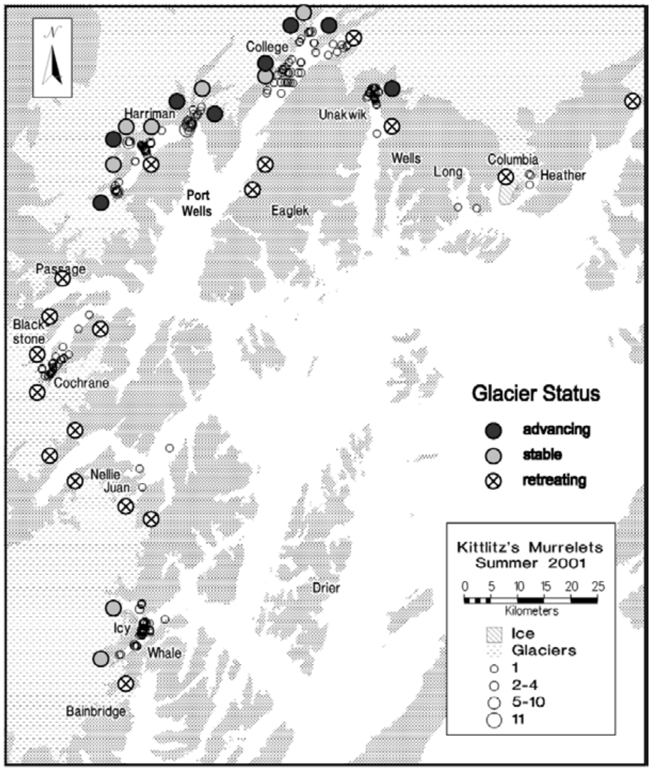

Fig. 4. Distribution of Kittlitz's Murrelets (open circles) during the 2001 intensive survey of Prince William Sound, and the status of tidewater and near-shore glaciers, based on Lethcoe (1987). Each circle represents an observation, with a different number of possible birds (1-11) per sighting.

most of which were classified in the 1980s as stable or advancing. Similarly, advancing or stable glaciers occurred at the terminus of Unakwik Inlet and Icy Bay, where we observed many Kittlitz's Murrelets. In other areas, glaciers were retreating by the 1980s, and of these, only Blackstone fjord retained substantial numbers of Kittlitz's Murrelet.

DISCUSSION

Kittlitz's Murrelets have declined dramatically in PWS during the 12 years of this study, and possibly for the past 30 years (Kendall & Agler 1998). However, little attention was given to this small, non-colonial bird until the 1989 *Exxon Valdez* oil spill, when it was

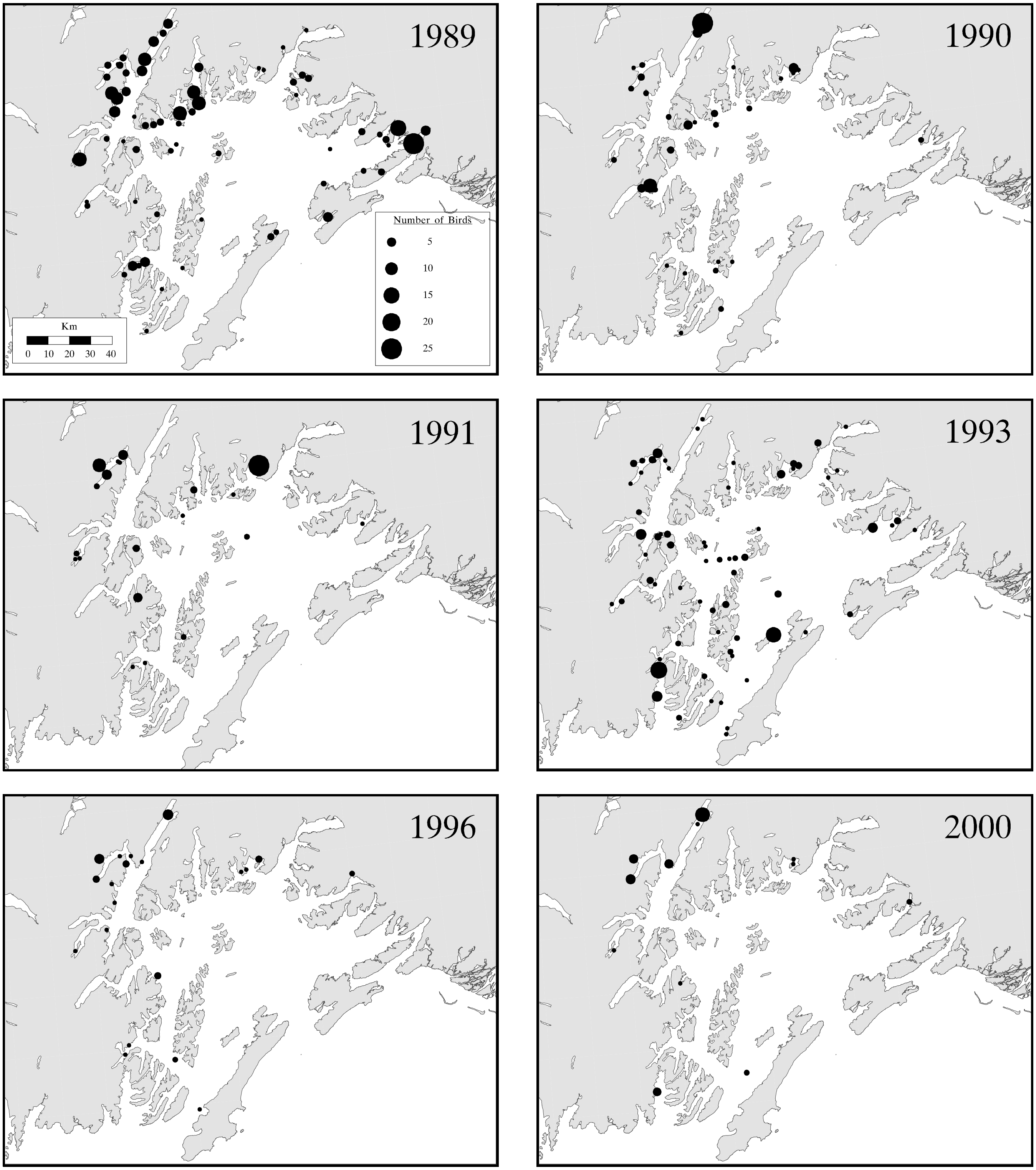

Fig. 5. Distribution of Kittlitz's Murrelets (filled circles) along randomly selected transects during the sound-wide surveys, 1989-2000. Each circle represents the total number of birds sighted on that transect.

suggested that, relative to its small population, it was the most affected species of marine bird (van Vliet & McAllister 1994). Since the oil spill, population trends in the GOA have been assessed in three other regions beyond PWS – the Kenai Fjords west of PWS (Van Pelt & Piatt 2003), the Malaspina Forelands east of PWS (USFWS 2003), and Glacier Bay farther south (Robards *et al*. 2003) – Kittlitz's Murrelets have declined dramatically in all of them. Little is known about their ecology and this paper is a step towards identifying the factors that may be influencing the population declines.

Distribution relative to glaciers

Our results support the observation that Kittlitz's Murrelets associate with tidewater glaciers (Isleib & Kessel 1973, Kendall & Agler 1998, Day *et al*. 1999, 2003), and more importantly, the hypothesis that their distribution is affected by glacier status. The northwest region of PWS contained ~ 30-45% of the estimated Kittlitz's Murrelet population through the mid-1990s, but today, it supports between 55% (based on 2000 sound-wide surveys) and 84% (2001 intensive survey) of the PWS population. The concentration in northwest PWS, where more glaciers are stable or advancing (Lethcoe 1987, Molnia 2001), suggests a strong association with the phase of advancement or recession exhibited by surrounding glaciers. In particular, Harriman fjord, with eight stable or advancing glaciers, supported ~ 58% of the estimated PWS population in 2001. The high number of 'healthy' (i.e., non-retreating) glaciers in this region is likely a consequence of the local topography, which promotes low atmospheric temperatures and high snow fall (Molnia 2001).

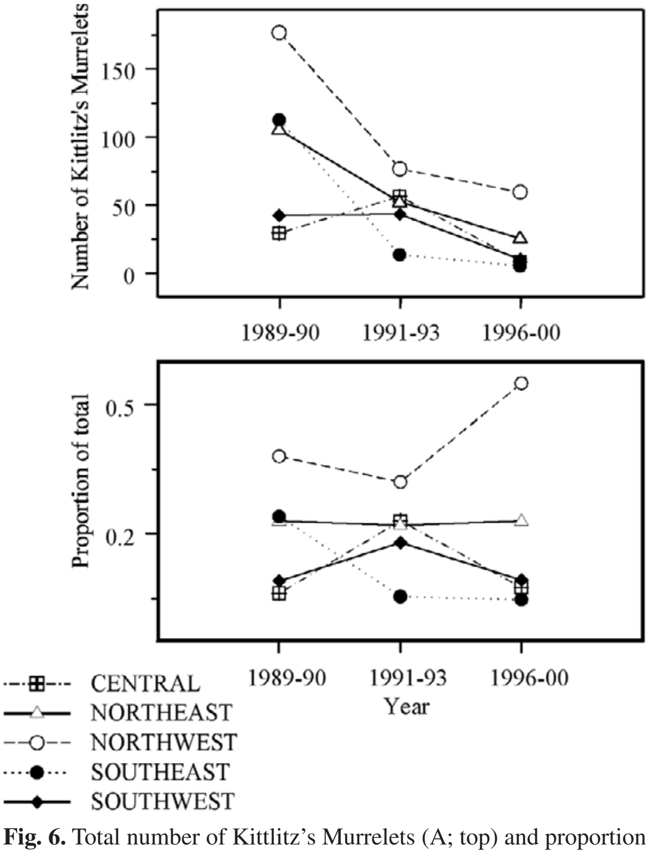

Fig. 6. Total number of Kittlitz's Murrelets (A; top) and proportion of total murrelets (B; bottom) for three time periods in five regions of Prince William Sound. Data are from the 1989-2000 sound-wide surveys.

The reported status of PWS glaciers was based on data from the mid or late 1980s (Lethcoe 1987), just prior to the decrease in the Kittlitz's population documented here. Many of these glaciers, however, have been retreating over at least the past 50 years (Lethcoe 1987, Molnia 2001, Arendt *et al*. 2002), and it is possible that the response of Kittlitz's Murrelet to changes in these glaciers began before our sound-wide surveys were initiated. Indeed, a PWS survey in 1972, using a different study design, revealed a population closer to 60 000 birds (63 229 ± 80 122 95% C.I.; Klosiewski & Laing 1994). The large confidence interval of this estimate requires caution in interpretation, but a population near that size in the early 1970s would suggest that Kittlitz's Murrelet has been declining in PWS over several decades.

The change in distribution of Kittlitz's Murrelet among PWS fjords in recent years may reflect changes in the fjords themselves. Among Alaskan glaciers, those in the Chugach Mountains have exceptionally high rates of volume change (Arendt *et al*. 2002). It is generally recognized that atmospheric temperature is linked to changes in glaciers (Root *et al*. 2003), but the connection is complicated by local topography and weather (Molnia 2001, Arendt *et al*. 2002). Physical and biological differences among the fjords themselves likewise may determine their attractiveness to Kittlitz's Murrelet. Even while only a few kilometers apart, neighboring fjords can vary tremendously because tidal effects, eddies, sediment load, and productivity depend on topography and drainage conditions, which are influenced by the glacier's movements (Svendsen 1995).

Biological link to glaciers

The attraction of Kittlitz's Murrelet to glacial outflow has been well documented (Day *et al*. 1999, 2003, this study), but the mechanisms responsible for this association remain unknown. In PWS, their near-exclusive use of tidewater glacier fjords suggests strong physical or biological links. The sparse information available on food preferences indicate that macrozooplankton and amphipods may at times comprise a large portion of their diet, but Kittlitz's Murrelets also show a high degree of dietary overlap with Marbled Murrelets (Day *et al*. 1999, Day & Nigro 2000). Kittlitz's Murrelets in PWS eat a variety of forage fish, including Pacific sandlance *Ammodytes hexapterus*, Pacific herring *Clupea pallasi*, and capelin *Mallotus villosus* (Day & Nigro 2000, Piatt unpublished data, KJK, pers. obs.). These prey species are available in many areas of PWS and rich forage sites outside the fjords attract Marbled Murrelets and other seabirds (Ostrand *et al*. 1998, Brown 2002, Ainley *et al*. 2003), suggesting that prey distribution is not entirely dictating the Kittlitz's Murrelet distribution. Day *et al*. (2003) proposed that Kittlitz's Murrelets, while remaining food generalists, have specialized to better compete for food in a habitat not easily exploited by other seabirds. They appear to select waters with low surface water clarity, and Day *et al*. (2003) speculated that their proportionately large eyes may be an adaptation to foraging under such conditions.

If Kittlitz's Murrelet is better adapted than other birds to forage in glacial waters with high sediment loads, they may have access to otherwise under-utilized resources. Macrozooplankton can be concentrated in dense patches in inner fjords via advection and entrapment by estuarine and tidally-induced currents (Weslawski *et al*. 2000, Zajaczkowski & Legezynska 2001), which might also attract fish. The undersides of icebergs and pack ice, and the upwelling that often occurs at glacial sills or at the face of a glacier, are small-scale features that can increase prey abundance or availability for seabirds (Hunt & Schneider 1987). The presence of ice alone, however, does not attract Kittlitz's Murrelet, since both retreating and advancing glaciers calve (Molnia 2001) and brash ice was present in areas without Kittlitz's (KJK, unpublished). Investigating the attributes of this dynamic foraging habitat will be critical to understanding the Kittlitz's ecology.

The mystery of why stable or advancing glaciers attract Kittlitz's Murrelet, while retreating glaciers do not, may require investigating differences in sedimentation rates and associated characteristics among glacier types. Fjords in the North Atlantic with receding glaciers tend to have higher sedimentation rates and lower salinity due to glacial ablation, which can lower primary productivity and diversity of benthos (Weslawski *et al*. 1995) and reduces the feeding ability and survival of macrozooplankton (Weslawski *et al*. 2000, Zajaczkowski & Legezynska 2001). The onset of the spring plankton bloom in fjords appears to depend partly on the resuspension of resting spores in the sediment, which might be impaired with increased sedimentation (Hegseth *et al*. 1995). A working hypothesis behind this physical-biological coupling is that the lack of a phytoplankton bloom and the increased mortality of macrozooplankton reduce the biomass of invertebrates and of forage fish. Kittlitz's Murrelets could thus be affected at multiple trophic levels, since they feed on euphausiids, amphipods, and small crustacea as well as fish. (Day *et al*. 1999, Day & Nigro 2000). The reduction in water transparency in fjords with retreating glaciers (Weslawski *et al*. 1995), might also reach a threshold where Kittlitz's Murrelet foraging success, even while adapted for low-visibility foraging, may be detrimentally affected.

Implications for the future

Recent analyses indicated that some PWS glaciers which had been categorized as stable or advancing (Lethcoe 1987), including five in the northwest region, shifted into receding phases in the 1990s (Molnia 2001, & pers. comm.). Our results suggest that continued wastage of these glaciers may precipitate future declines in the PWS Kittlitz's Murrelet population. Similarly, the decline of Kittlitz's Murrelet populations in other regions of the GOA can be expected to continue, particularly if glacial recession lags nearly half a century behind changes in climate (Arendt *et al*. 2002).

Kittlitz's Murrelets inhabit some non-glacial areas of Alaska (Day *et al*. 1999), but these populations are small and possibly isolated, as indicated by the genetic distinctiveness identified between populations in the Aleutian Islands and the northern GOA (Pitocchelli *et al*. 1995). Kittlitz's Murrelet is thought to have evolved during the Pleistocene (Pitocchelli *et al*. 1995, Friesen *et al*. 1996), and thus to have survived periods of glacial recession. However, Root *et al*. (2003) noted that for such species the cumulative effects of rapid environmental change, worsened by habitat loss, fragmentation of populations, and other anthropogenic impacts, are unprecedented. In addition to changes in their habitat, Kittlitz's Murrelets are confronted with oil spills and incidental take in gillnets, and possibly, disturbance from increased boat traffic near tidewater glaciers (Day *et al*. 1999, 2003, USFWS 2003). The cumulative effects of these stressors could impinge on the ability of some Kittlitz's Murrelet populations to adapt to global warming.

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REFERENCES

AINLEY, D.G., FORD, R.G., BROWN, E.D., SURYAN, R.M. & IRONS, D.B. 2003. Prey resources, competition, and geographic structure of kittiwake colonies in Prince William Sound. *Ecology* 84: 709-723.

ARENDT, A.A., ECHELMEYER, K.A., HARRISON, W.D., LINGLE, C.S. & VALENTINE, V.B. 2002. Rapid wastage of Alaska glaciers and their contribution to rising sea level. *Science* 297: 382-386.

BROWN, E.D. 2002. Life history, distribution, and size structure of Pacific capelin in Prince William Sound and the northern Gulf of Alaska. *ICES Journal of Marine Science* 59: 983-996.

COCHRAN, W.G. 1977. Sampling techniques. John Wiley and Sons, New York.

DAY, R.H. & NIGRO, D. 1999. Status and ecology of Kittlitz's murrelet in Prince William Sound, 1996-1998. *Exxon Valdez* Oil Spill Restoration Project Final Report (Restoration Project 98142), ABR, Inc., Fairbanks, Alaska.

DAY, R.H. & NIGRO, D.A. 2000. Feeding ecology of Kittlitz's and marbled murrelets in Prince William Sound, Alaska. *Waterbirds* 23: 1-14.

DAY, R.H., KULETZ, K.J. & NIGRO, D.A. 1999. Kittlitz's murrelet (*Brachyramphus brevirostris*). In: The Birds of North America, No. 435. Poole, A. & Gill, F (Eds.). Philadelphia: The Birds of North America.

DAY, R.H., PRICHARD, A.K. & NIGRO, D.A. 2003. Ecological specialization and overlap of *Brachyramphus* murrelets in Prince William Sound, Alaska. *Auk* 120: 680-699.

FRIESEN, V.L., PIATT, J.F. & BAKER, A.J. 1996. Evidence from Cytochrome b sequences and allozymes for a "new" species of alcid: the Long-billed Murrelet (*Brachyramphus perdix*). *Condor* 98: 681-690.

GAY, S.M. & VAUGHAN, S.L. 1998. Descriptive physical oceanography of bays and fjords in Prince William Sound, Alaska used as nursery habitat by juvenile Pacific herring (*Clupea pallasi*). *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 96320-M), Prince William Sound Science Center, Cordova, Alaska, 99574).

HEGSETH, E.N., SVENDSEN, H. & VON QUILLFELDT, C.H. 1995. Phytoplankton in fjords and coastal waters of northern Norway: environmental conditions and dynamics of the spring bloom. In: Skjoldal, H.R., Hopkins, C., Erikstad, K.E. & Leinaas, H.P. (Eds.). Ecology of Fjords and Coastal Waters. Elsevier, New York: pp. 45-72, HUNT, G.L., Jr. & SCHNEIDER, D.C. 1987. Scale-dependent processes in the physical and biological environment of marine birds. In: Croxall, J. P. (Ed). Seabirds: feeding ecology and role in marine ecosystems. Cambridge University Press, Cambridge, England, Great Britain: pp. 7-41.

ISLEIB, M.E. & KESSEL, B. 1973. Birds of the North-Gulf Coast-Prince William Sound Region, Alaska. *Biological Papers of the University of Alaska* 14: 1-149.

KENDALL, S.J. & AGLER, B.A. 1998. Distribution and abundance of Kittlitz's murrelets in southcentral and southeastern Alaska. *Waterbirds* 21: 53-60.

KLOSIEWSKI, S P. & Laing, K.K. 1994. Marine bird populations of Prince William Sound, Alaska, before and after the *Exxon Valdez* oil spill. Final report, Natural Resource and Damage Assessment Bird Study No. 2. U.S. Fish and Wildlife Service, Anchorage, Alaska.

KULETZ, K.J., LABUNSKI, E.A. & BRENNEMAN, K.M. 2003. Distribution and abundance of Kittlitz's Murrelets in Prince William Sound, Alaska, in summer 2001. Unpublished Report, U. S. Fish and Wildlife Service, Anchorage, Alaska.

LANCE, B.K., IRONS, D.B. KENDALL, S.J. & MCDONALD, L.L. 2001. An evaluation of marine bird population trends following the *Exxon Valdez* Oil Spill, Prince William Sound, Alaska. *Marine Pollution Bulletin* 42: 298-309.

LETHCOE, N.R. 1987. An observer's guide to the glaciers of Prince William Sound, Alaska. Prince William Sound Books, Valdez, AK.

MOLNIA, B. 2001. Glaciers of Alaska. Alaska Geographic vol. 28, no.2. Alaska Geographic Society, Anchorage, Alaska.

NIELSON, R., HOWLIN, S. & MCDONALD, L. 2003. Bootstrapping to investigate effects of sample size on variance and bias of estimated species totals for Prince William Sound Marine Bird Surveys. Unpublished Report by Western Ecosystems Technology, Inc. for the U.S. Fish and Wildlife Service, Anchorage, Alaska.

OSTRAND, W.D., COYLE, K.O., DREW, G.S., MANISCALCO, J.M. & IRONS, D.B. 1998. Selection of forage fish schools by murrelets and Tufted Puffins in Prince William Sound, Alaska. *Condor* 100: 286-297.

PITOCHELLI, J., PIATT, J.F. & CRONIN, M. 1995. Morphological and genetic divergence among Alaskan populations of Brachyramphus murrelets. *Wilson Bulletin* 107: 235-250.

ROBARDS, M., DREW, G., PIATT, J., ANSON, J.M., ABOOKIRE, A., BODKIN, J., HOOGE, P. & SPECKMAN, S. 2003. Ecology of selected marine communities in Glacier Bay: Zooplankton, forage fish, seabirds and marine mammals. Final report to Glacier Bay National Park and Preserve (Gustavus, Alaska). USGS Alaska Science Center, Biological Science Office, Anchorage, Alaska.

ROOT, T.L., PRICE, J.T., HALL, K.R., SCHNEIDER, S.H., ROSENZWEIG, C. & POUNDS, J.A. 2003. Fingerprints of global warming on wild animals and plants. *Nature* 421: 57-60.

STEPHENSEN, S.W., IRONS, D.B., KENDALL, S.J. LANCE, B.K. & MCDONALD, L.L. 2001. Marine bird and sea otter population abundance of Prince William Sound, Alaska: Trends following the *T/V Exxon Valdez* Oil Spill, 1989-2000. *Exxon Valdez* Oil Spill Restoration Project Annual Report (Restoration Project 00159), U.S. Fish and Wildlife Service, Anchorage, Alaska.

SVENDSEN, H. 1995. Physical oceanography of coupled fjord-coast systems in northern Norway with special focus on frontal dynamics and tides. In: Skjoldal, H. R., Hopkins, C., Erikstad, K.E. & Leinaas, H.P. (Eds.). Ecology of Fjords and Coastal Waters. Elsevier, New York: pp. 149-164.

USFWS. 2003. Candidate and Listing Priority Assignment for Kittlitz's Murrelet. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska. 38 pp.

VAN PELT, T.I. & PIATT, J.F. 2003. Population status of Kittlitz's and Marbled Murrelets and surveys for other marine bird and mammal species in the Kenai Fjords area, Alaska. Unpubl. Report, Alaska Science Center, USGS, Anchorage, Alaska.

VAN VLIET, G.B. 1993. Status concerns for the 'global' population of Kittlitz's Murrelet: is the 'glacier murrelet' receding? *Pacific Seabird Group Bulletin* 20: 15-16.

VAN VLIET, G. & MCALLISTER, M. 1994. Kittlitz's Murrelet: the species most impacted by direct mortality from the *Exxon Valdez* oil spill? *Pacific Seabirds* 21: 5-6.

WALTHER, G.R., POST, E., CONVEY, P., MENZEL, A., PARMESAN, C., BEEBEE, T.J.C., FROMENTIN, J.M., HOEGH-GULDBERG, O. & BAIRLEIN, F. 2002. Ecological responses to recent climate change. *Nature* 416: 389-395.

WESLAWSKI, J.M., KOSZTEYN, J. ZAJACZKOWSKI, M., WIKTOR, J. & KWASNIEWSKI, S. 1995. Fresh water in Svalbard fjord ecosystems. In: Skjoldal, H. R., Hopkins, C., Erikstad, K.E. & Leinaas, H.P. (Eds.). Ecology of Fjords and Coastal Waters. Elsevier, New York: pp. 229-242,.

WESLAWSKI, J.M., PEDERSEN, G., PETERSEN S.F. & PORAZINSKI, K. 2000. Entrapment of macroplankton in an Arctic fjord basin, Kongsfjorden, Svalbard. *Oceanologia* 42: 57-69.

WILSON, J.G. & OVERLAND, J.E. 1986. Meteorology. In: Hood, D.W. & Zimmerman, S.T. (Eds.). The Gulf of Alaska: physical environment and biological resources. Anchorage: US Dep. Commerce, National Oceanic and Atmospheric Administration, Ocean Assessments Division: pp. 31- 54.

ZAJACZKOWSKI, M.J. & LEGEZYNSKA, J. 2001. Estimation of zooplankton mortality caused by an Arctic glacier outflow. *Oceanologia* 43: 341-351.

ADVECTION, PELAGIC FOOD WEBS AND THE BIOGEOGRAPHY OF SEABIRDS IN BERINGIA

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SUMMARY

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Despite its great distance from productive shelf-edge habitat, the inner shelf area of the Bering Sea, from St. Lawrence Island to the Bering Strait, supports a surprisingly large number (>5 million) of seabirds during summer, mostly small plantivorous auklets (65%) and large piscivorous murres (19%) and kittiwakes (5%). This paradox of seabird biogeography is explained by the Anadyr "Green Belt" - a current that advects nutrients and plankton over 1200 km from the outer Bering Sea shelf-edge to the central Chukchi Sea. Turbulent upwelling of this nutrient-rich water at Anadyr and Bering straits further enhances high levels of primary production (360 gC $m^{-2}y^{-1}$) and helps sustain the enormous biomass of zooplankton entrained in the Anadyr Current. Primary production in adjacent waters of the Chukchi Sea (420 gC $m^{-2}y^{-1}$) exceeds that observed below Bering Strait, and zooplankton are equally abundant. Auklets account for 49% of total food consumption below Bering Strait (411 mt d^{-1}), whereas piscivores dominate (88% of 179 mt d^{-1}) in the Chukchi Sea. Of 2 million seabirds in the Chukchi region, auklets (6%) are supplanted by planktivorous phalaropes (25%), and piscivorous murres (38%) and kittiwakes (15%). Average carbon flux to seabirds (0.65 mgC $m^{-2}d^{-1}$) over the whole region is more typical of upwelling than shelf ecosystems. The pelagic distribution of seabirds in the region appears to be a function of advection, productivity and water column stability. Planktivores flourish in areas with high zooplankton concentrations on the edge of productive upwelling and frontal zones along the "Green Belt", whereas piscivores avoid turbulent, mixed waters and forage in stable, stratified waters along the coast and in the central Chukchi Sea.

Keywords: Bering Sea, Chukchi Sea, seabird, auklet, murre, zooplankton, production, Green Belt, planktivore, piscivore, food web, carbon flux, Alaska, North Pacific

INTRODUCTION

The continental shelf of the northern Bering Sea and Chukchi Sea-encompassing Bering Strait- constitutes the largest shelf sea and one of the most productive biological regimes in the world (Coachman & Shigaev 1992). Northward flow of nutrient-rich oceanic water in the Anadyr Current, which originates far to the south, in the basin of the Bering Sea, promotes extremely high primary productivity and transports great numbers of oceanic zooplankton across the western and central portion of the region (Springer *et al*. 1989, Springer & McRoy 1992). The northward advection of nutrients and biomass, or "Green Belt" (Springer *et al*. 1996), in turn sustains a huge biomass of benthic invertebrates (Grebmeier *et al*. 1988), marine mammals (Frost & Lowry 1981) and seabirds (Springer *et al*. 1987) in the region. This rich oceanic environment contrasts with the relatively impoverished coastal zone of the eastern shelf, which owes its' character to the nutrient-poor water advected north in the Alaska Coastal Current (Coachman *et al*. 1975). Food web productivity and species diversity are both low by comparison to the oceanic regime (Springer *et al*. 1987, 1989, Grebmeier *et al*. 1988, Springer & McRoy 1992).

The feeding ecology of seabirds and their pelagic distribution in relation to local oceanographic features of this region have been reasonably well described (Bedard 1969, Springer *et al*. 1984, Springer & Roseneau 1985, Piatt *et al*. 1990a, 1991, 1992; Harrison 1990, Hunt & Harrison 1990, Hunt *et al*. 1990, Haney 1991, Schauer 1991, Elphick & Hunt 1993, Russell *et al*. 1999). In the first overview of seabird ecology for the region, Springer *et al*. (1987) showed that two distinct environmental settings in the northern Bering-Chukchi ecosystem lead to characteristic pathways of energy flow through pelagic food webs to avian consumers. The diversity and abundance of nesting seabirds are much higher in the western region dominated by oceanic water, than in the eastern region dominated by coastal water. For example, some of the largest colonies in the world of primarily planktivorous Least Auklets *Aethia pusilla*, Crested Auklets *A. cristatella*, and Parakeet Auklets *A. psittacula* and primarily piscivorous Common Murres *Uria aalge* and Thick-billed Murres *Uria lomvia* are found on St. Lawrence Island and the Diomede islands. In contrast, only Parakeet Auklets nest in the coastal zone of the northeastern Bering Sea, and in small numbers, there are very few Thick-billed murres, and abundances of other species also are low (Sowls *et al* 1978).

In this paper, we examine how oceanography and biology influence the pelagic distribution and ecology of seabirds throughout Beringia. We examine seabird diversity and abundance at sea using data collected on seabirds during the 1970s and 1980s by the U.S. Fish and Wildlife Service (USFWS) as part of the Outer Continental Shelf Environmental Assessment Program (OCSEAP). We analyze the distribution of planktivorous and piscivorous seabird species that occur in the region during summer, measure the carbon flow through seabird communities on a sub-regional basis, and consider the observed patterns of seabird distribution at sea with respect to published information on oceanography, primary and secondary productivity, and pelagic fish communities. This overview of pelagic seabird ecology in the northern Bering and Chukchi seas represents a relatively rare attempt to integrate seabird biogeography with respect to topography, oceanography, and productivity over basin-wide spatial scales in Alaska (e.g., Schneider *et al*. 1986).

METHODS

Surveys for seabirds were conducted on ships of opportunity between 1976 and 1984 using protocols developed by the USFWS (Gould & Forsell 1989). Seabirds were censused in a 300 m-wide strip on the left or right of the ship's center line and over a 10-min time interval (a transect). Numbers of all birds swimming on the water were recorded by species. Instantaneous counts of flying birds were made three times during a 10-min transect, which combined with counts of sitting birds, provided the total numbers of birds per transect with which to calculate densities (numbers/km^2). Areas were determined from strip width, time traveled and ship speed. Ancillary data on bird behavior, weather and sea conditions, ship position, etc., were collected for each transect. For details on methods and sources of data, see Gould & Forsell (1989) or go online to the North Pacific Pelagic Seabird Database (NPPSD) at http://www.absc.usgs.gov/research/NPPSD/ where all the data used in this analysis are compiled.

Analyses and mapping of bird distributions and abundance were accomplished with a GIS system designed for working with marine bird and mammal data (Computer Aided Mapping and Resource Inventory System (CAMRIS, copyright 1987, 1988 by R. Glenn Ford Consulting Inc., Portland OR, www.camris.com). For mapping, and for estimating bird abundance, transect data were binned into selected latitude-longitude blocks and the average density (birds km^{-2}) for each species was calculated from strip transects (length times width) falling within the block. Density polygons were generated as contoured isopleths of density, and missing blocks were extrapolated from the densities of adjacent blocks. Missing blocks were not filled if they were more than 1 block away from a block containing data. Bird abundance was estimated (mean density times area) for 30˚ latitude-longitude blocks. Maps of distribution are presented as density contour isopleths generated from a grid of 15° latitude-longitude blocks and scaled geometrically.

USFWS transects conducted in June through September were used to calculate summer densities of species and to map their distributions. For purposes of examining biogeography, data were grouped over all years. In areas with sufficient transects to examine inter-annual variability, patterns of distribution for common species were similar among years. About 3160 km^2 of area were surveyed on a total of 2630 strip transects. The region was divided into three sub-regions for analysis: St. Lawrence Island- lower Chirikov Basin (SLI-CB), an area of 99 470 km^2 bounded by 62° 30' N, 64° 30' N, 164° 00' W, and 174° 00' W; the Bering Strait (BER-STR), an area of 55 437 km^2 bounded by 64° 30' N, 67° 00' N, 164° 00' W, and 171° 00' W; and the central/eastern Chukchi Sea (CHUKCHI), an area of 61 753 km^2 bounded by 67° 00' N, 69° 30' N, 164° 00' W, and 170° 30' W. Survey effort was widely distributed throughout the sub-regions, except for areas west of the International Convention Line separating U.S. and Russian waters, where few or no surveys were conducted. To estimate regional bird populations, data were first binned into 165 30' x 30' latitude-longitude blocks, so that 95%, 94%, and 100% of blocks were sampled in sub-regions SLI-CB, BER-STR, and CHUKCHI, respectively. Abundance in each sub-region was then calculated by summing the totals in each 30° block (mean number of birds times block area) over the marine area sampled in each sub-region.

TABLE 1
Body mass and field metabolic rate (FMR) of seabird species or genera found in the northern Bering Sea and Chukchi Sea.

Common Name	Code	Scientific Name (g) (kJ/d) type*	Mass	FMR	Food
Northern Fulmar	NOFU	*Fulmarus glacialus*	620	991	O
Short-tailed Shearwater	STSH	*Puffinus tenuirostris*	610	980	O
Pelagic Cormorant	PECO	*Phalacrocorax pelagicus*	1800	1972	F
Red Phalarope	REPH	*Phalaropus fulicaria*	55	207	P
Jaeger (spp.)	UNJA	*Stercorarius* spp.	490	851	F
Herring Gull	HEGU	*Larus argentatus*	1130	1460	F
Glaucous Gull	GLGU	*Larus hyperboreus*	1410	1684	F
Black-legged Kittiwake	BLKI	*Rissa tridactyla*	420	770	F
Arctic Tern	ARTE	*Sterna paradisaea*	120	343	F
Pigeon Guillemot	PIGU	*Cepphus columba*	530	895	F
Tufted Puffin	TUPU	*Fratercula cirrhata*	800	1168	O
Horned Puffin	HOPU	*Fratercula corniculata*	540	906	F
Kittlitz's Murrelet	KIMU	*Brachyramphus brevirostris*	240	537	F
Murre (spp.)	UNMU	*Uria* spp.	980	1331	F
Parakeet Auklet	PAAU	*Aethia psittacula*	290	606	P
Least Auklet	LEAU	*Aethia pusilla*	90	285	P
Crested Auklet	CRAU	*Aethia cristatella*	300	620	P

* Food type - predominant food (by volume) taken by species during the breeding season: O= omnivorous (fish and plankton); F= fish; P= plankton.

Alaskan seabird colony data were obtained from USFWS archives (provided by A. Sowls, Alaska Maritime National Wildlife Refuge, Homer, Alaska), which included updated colony estimates from Sowls *et al*. (1978). Order of magnitude estimates of Siberian seabird colony populations were provided by N. Konyukhov and L. Bogoslovskaya (Institute of Evolutionary Ecology and Morphology of Animals, Moscow). Estimates of seabird populations on Big Diomede Island (V. Zubakin, A. Kondratiev, and J. Piatt, unpubl. data) and Little Diomede Island (A. Fowler and S. Hatch, unpubl. data) were obtained during joint U.S.-Russian studies in 1991.

An allometric equation was used to estimate daily individual energy requirements for each seabird species (Table 1), based on the measured field metabolic rates (FMR) of seabirds in cold ocean environments (Birt-Friesen *et al*. 1989): $\log_{10}$ FMR = 3.13 ± 0.646 * $\log_{10}$ [mass (in kg)]. Body masses vary over time and geographically, as well as between sexes in dimorphic species. Body masses (±5 g) during the breeding season were obtained from USFWS data archives and from published sources (Dunning 1984, Piatt *et al*. 1990a, 1991). Unweighted mean weights of sexes were calculated for sexually dimorphic species. For generic groups not distinguished or grouped in the at-sea data set (2 murres, 3 jaegers), unweighted means of species' weights were used for calculations. From FMR's, average daily energy intake was calculated (Schneider *et al*. 1986) for each species as: E intake (in kJ m^{-2} d^{-1}) = 1.33*FMR*(birds per unit area); where 1.33 is the ratio of energy ingested to energy assimilated. Numbers of birds estimated from ship-based surveys rather than colony surveys were used in these calculations. Conversion factors of 20.9 kJ g^{-1} dry and 0.4 gC g^{-1} dry were used to convert energy transfer to mass transfer (Schneider *et al*. 1986). Conversion factors of 0.20, 0.27, and 0.24 g(dry)/g(wet) were used to estimate wet weight consumption of food biomass by planktivores, piscivores, and omnivorous species (Table 1), respectively (Wiens & Scott 1975). We did not calculate the additional food requirements of chicks at colonies owing to a lack of local production and diet data for many species. In most cases these would be small relative to needs of adult and non-breeding members of populations thoughout the breeding season.

The image of sea surface temperature (SST) was developed using data from advanced very high-resolution radiometer (AVHRR) sensors aboard NOAA Polar Orbiting Satellites. For this report, we selected the best single "cloud-free image" available in the month of July during 1991, when we were concurrently doing surveys for auklets in Bering Strait (Piatt *et al*. 1992). Raw AVHRR data was calibrated and georeferenced at the Alaska Science Center.

BACKGROUND: OCEANOGRAPHY

Water masses

Based on extensive sampling of water masses in the northern Bering and Chukchi seas over many years from the 1950s to 1980s and numerous measures of current flow, the oceanography of the region during summer is well known. Three distinct water masses (Fig. 1), each with different origins, move northward through the Bering Strait (Fleming & Heggarty 1966, Coachman *et al*. 1975, Coachman 1993, Stabeno *et al*. 1999). Anadyr Water, a "river" of cold, high-salinity (ca. 32.8-33.0 ppt), nutrient-laden oceanic water that originates along the slope of the Bering Sea continental shelf, flows northward through Anadyr Strait and western Bering Strait, and finally into the central Chukchi Sea where it blends with Bering Shelf Water (Figs. 2 & 3). As much as 72% of the water transported through Bering Strait during summer may come through Anadyr Strait (Overland & Roach 1987). Alaska Coastal Water originates in the Gulf of Alaska. This low salinity (ca. <32.0 ppt), seasonally warm water hugs the Alaskan coast and retains its character as it transits the Bering and Chukchi seas (Figs. 2 & 3). It is influenced by freshwater runoff from major rivers (e.g., Yukon), particularly in summer. Bering Shelf Water is the resident water mass of the central shelf region south of St. Lawrence Island. Intermediate in character (ca. 32.0-32.8 ppt) between Anadyr and Alaska Coastal waters, Bering Shelf Water is advected northward around both sides of St. Lawrence Island, and then flows through Bering Strait where it eventually blends with Anadyr Water and Alaska Coastal Water (Figs. 2 &3).

Currents

Current flow through Bering Strait is almost always in a northerly direction, particularly in summer. Residence times of Anadyr Water in the Chirikov Basin range from 10-20 d in July, in contrast to 20-50 d in late August-September (Coachman & Shigaev 1992). Currents flow faster at points of topographic constriction (Anadyr, Shpanberg, and Bering straits) and around major headlands; and slower in the meanders, eddies, and gyres that form downstream from those points (Fig. 2). In the absence of significant wind stress, currents are fastest in the Bering Strait (Overland & Roach 1987), particularly in the compressed Alaska Coastal Current where flow rates range from 50-150 cm sec^{-1}.

The Anadyr Current is a topographic boundary current. In the Gulf of Anadyr, it is steered in a clockwise direction along the 50 m isobath (Fig. 1) and transit time to Anadyr Strait is about one month. Most Anadyr Water enters Anadyr Strait, but some continues east around the south side of St. Lawrence Island where it mixes with Bering Shelf Water. More recent evidence suggests that nutrient-rich slope water may enter Anadyr Strait from the

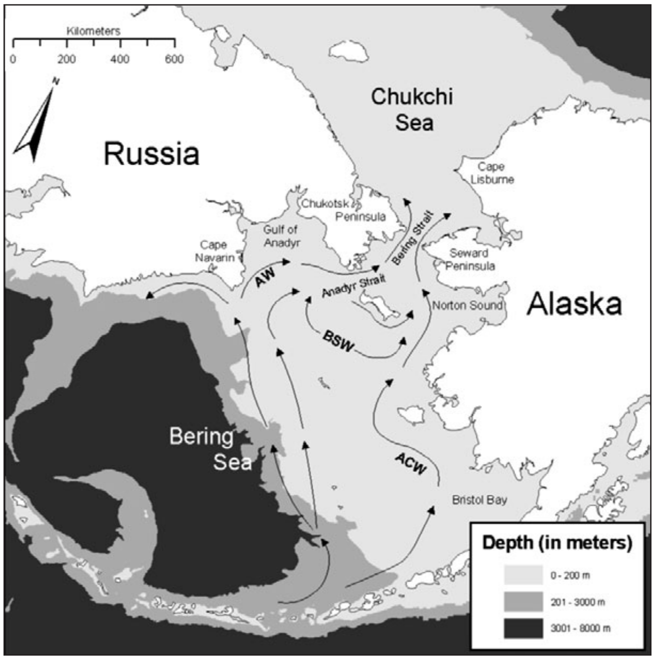

Fig. 1. The Bering and Chukchi seas, with circulation patterns and origins of the principal water masses flowing north through Bering Strait. See text for sources. AW - Anadyr Water; BSW - Bering Shelf Water; ACW - Alaska Coastal Water.

outer Bering Sea Shelf, after having been advected onto the shelf at lower latitudes (Stabeno *et al*. 1999). Whatever its' origin, "Anadyr" water flows through the canyon in the Chirikov Basin leading north to the Bering Strait. After emerging from Bering Strait, the deep "core" of Anadyr Water is diverted to the west along the 50 m isobath (Figs. 1 & 2). Upper water layers continue to move northward where they converge with westward flowing Bering Shelf/Anadyr waters (Coachman *et al*. 1975). Alaska Coastal Water follows 20-30 m isobaths throughout its transit of the Bering Sea and into the Chukchi Sea where it veers sharply to the east towards Kotzebue Sound before continuing northward along the coast, around Pt. Hope, and into the Beaufort Sea. Bering Shelf Water is advected northward around both ends of St. Lawrence Island and may be disrupted by westward expansion of the Alaska Coastal Current or by eastward expansion of the Anadyr Current. Northward flow continues through the Chirikov Basin, and clearly identifiable Bering Shelf Water is sandwiched between Alaska Coastal and Anadyr waters as they transit Bering Strait.

Owing to mixing in the Bering Strait, Bering Shelf Water may become indistinguishable from Anadyr Water in the Chukchi Sea. Termed Shelf/Anadyr water, there is a divergence of this flow from the deep Anadyr core above the Bering Strait (Fig. 2). Shelf/Anadyr water loops to the east as it winds around the 30 m contour toward Kotzebue Sound, before turning northwest off Pt. Hope (Coachman & Shigaev 1992). A pool of Shelf/Anadyr water (typically 32.2-32.6 ppt) forms between the flows of Shelf/Anadyr water and the Anadyr core, and is noted as a center for extremely high primary production (see below). The exact location of the pool appears to vary considerably over time (Springer & McRoy 1992).

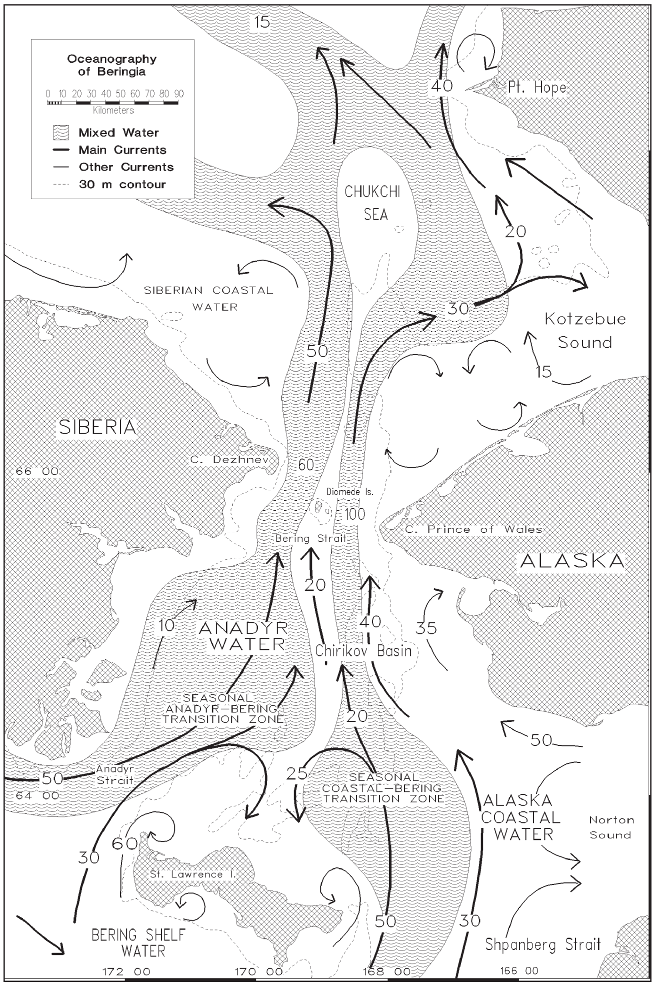

Fig. 2. Detailed oceanography of Beringia. "Mixed Water" shading shows the seasonal range in location of un-stratified water in the turbulent Anadyr current and in the transition zone between Bering Shelf and Alaska Coastal waters (drawing modified from Coachman *et al*. 1975, Grebmeier and McRoy 1989). Numbers = current speed in cm sec^{-1}.

Eddies and gyres are very common in the Bering Strait (Coachman *et al*. 1975) and in other regions of Alaska where strong currents flow past islands and mainland promontories (Schumacher & Kendall 1991). Persistent barotropic (pressure-driven) eddies form downstream from major headlands and islands (St. Lawrence Island, Cape Prince of Wales, Pt. Hope, etc.).

Transitional waters

Anadyr, Bering Shelf, and Alaska Coastal waters are arranged sequentially from west to east in Bering Strait (Fig. 2). There is little lateral mixing or diffusion in the system. Transition zones between water masses are often less than 10 km in width in areas of strong current flow (Coachman & Shigaev 1992). However, the width and location of these boundaries may vary considerably over summer as winds, tides, and freshwater runoff influence current regimes, water mass volume, and vertical stratification (Fig. 2). An eastward bulge of Anadyr Water and a westward bulge of Alaska Coastal Water are persistent features in Chirikov Basin.

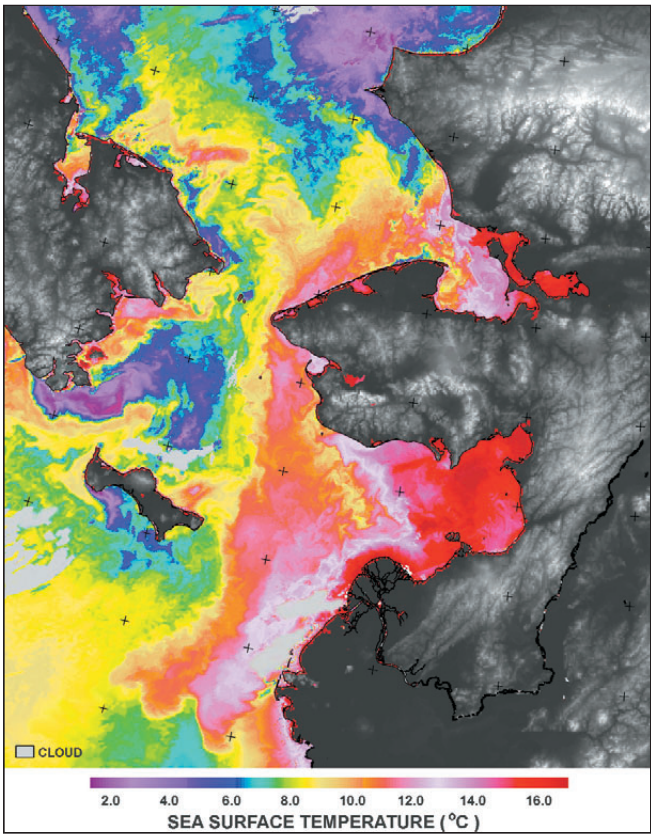

Fig. 3. Sea surface temperatures in the northern Bering and Chukchi seas, July 6, 1991. The image was developed using data from Advanced Very High-Resolution Radiometer (AVHRR) satellite sensors (courtesy of David Douglas, USGS).

Transitional water between coastal and shelf waters is well-defined as a zone of mixed water fronting two stratified water masses on each side (e.g., see Harrison & Hunt 1990). The transition zone between Bering Shelf and Anadyr waters is harder to define because Anadyr Water is already mixed by upwelling turbulence. Any attempt to illustrate mixed water zones in Beringia (e.g., Fig. 2) must therefore allow for the seasonal movements of transition zones between currents, and seasonal changes in size and strength of currents. In contrast, an instantaneous AVHRR snapshot of sea surface temperatures (Fig. 3) reveals only some of the known features, i.e., a sharp transition between Coastal and Bering Shelf waters, and an eastward bulge of cold, Anadyr water above St. Lawrence Island.

Stratification and mixing

In all waters, summer warming of the sea surface leads to vertical stratification and stability of the water column. Pycnoclines range from 10-20 m in depth in most areas. Stratification is greatly enhanced by freshwater runoff, which reduces the salinity of the surface layer and dramatically increases structural stability of the water column. In addition, vertical heat flux to deep water is inversely related to vertical salinity gradients, so that freshwater runoff promotes further warming of surface layers, thermal stratification, and water column stability (Coachman *et al*. 1975). Thus, Alaska Coastal Water is typically an order of magnitude more stable than Bering Shelf Water, and AVHRR imagery reveals little upwelling of cooler water in the Alaska Coastal Current until it enters the northern Chukchi (Fig. 3). Fresh water from rivers and melting ice along the Siberian coast also tends to warm and stratify a narrow band of Anadyr Water along that shore. Layering and eddies are very common in waters entering Bering Strait, but are destroyed by downstream turbulence in and just north of the strait (Coachman *et al*. 1975, Coachman & Shigaev 1992).

Mixing of the water column occurs at current boundary fronts, because of topographically induced upwelling. Winds can mix surface waters in any water mass, and this occurs regularly in summer with passing storms. Owing to the difference in densities between water masses, strong fronts form at the borders of Alaskan Coastal, Bering Shelf, and Anadyr waters. Frontal zones between water masses may contain completely mixed and unstratified water, with upwelling or downwelling at the boundaries. Topographically induced upwelling is a major source of mixing in the Bering Strait region. The Anadyr Current speeds up as it constricts in Anadyr Strait, and a tremendous amount of kinetic energy is converted to turbulent energy as water enters the shallow Chirikov Basin (Fig. 1). The result is a large plume of cold, well-mixed water downstream of the strait (Fig. 2), readily apparent in most AVHRR images of the region (Fig. 3). Any layering or stratification that develops in Chirikov Basin is broken down again as water passes through Bering Strait, and another plume of mixed water forms downstream. Minimum stratification is always observed directly downstream from Anadyr and Bering straits (Coachman & Shigaev 1992). Upwelling also occurs close to shore around St. Lawrence and Diomede islands (Springer & Roseneau 1985, Piatt *et al*. 1992).

BACKGROUND: BIOLOGICAL PRODUCTION

Nutrients and primary production

Primary production in the northern Bering and Chukchi Sea ecosystem is largely a function of three factors: nutrient concentrations, water column stability and light (Sambrotto *et al*. 1984, Springer *et al* 1996). Advection plays the over-riding role in determining nutrient levels and production along this northern branch of the "Green Belt" (Springer *et al*. 1996). Three major production centers are recognized (Springer & McRoy 1992, Coachman & Shigaev 1992). The first center is in the large gyre of Anadyr Water in the Gulf of Anadyr (Fig. 4), which originates at depth over the slope and outer continental shelf (beginnings of the "Green Belt"), flows up onto the north-western shelf near Cape Navarin, circles the Gulf of Anadyr and continues north through Bering Strait and into the Chukchi Sea. Production is initiated when nutrients from deep waters rise into the euphotic zone as the Anadyr Current shoals off Cape Navarin (Figs. 1 & 4). Downstream of the upwelling, stratification develops in the upper water layers and primary production at the center of the gyre attains 700 g C m^{-2} yr^{-1}. As the Anadyr current transits the northern gulf, lateral mixing reduces stratification, thus diminishing production (Coachman & Shigaev 1992).

Although it is not evident from the synoptic (August, 1988) cruise data presented in Fig. 4, Anadyr Water in Anadyr Strait can have extremely high production levels (800+ mg m^{-2} chlorophyll), although production drops rapidly with distance from the strait (Springer & McRoy 1992). This occurs in a relatively small area where Siberian coastal freshwater runoff creates stratification and stability in the water column in Anadyr Strait (Coachman *et al*. 1975). Thus, the north side of Anadyr Strait, though small in area, is a high production center. In addition, production is often quite high (50-200 mg m^{-2} chlorophyll) close to the west and east coasts of St. Lawrence Island (Springer & McRoy 1992) because in water depths of 20-30 m light penetrates below the nutricline and into fingers of Anadyr Water. Turbulent mixing in Anadyr Strait interrupts the developing bloom but "resets" the system, allowing another center of high production (up to 770 g C m^{-2} y^{-1}) to form downstream in the northern Chirikov Basin (Springer *et al*. 1996). Production is enhanced because freshwater runoff from Siberia layers over denser Anadyr Water and results in thermal stratification along the coast (see Fig. 3), which serves to increase stability of the water column just south of the Bering Strait (Coachman & Shigaev 1992).

Turbulence through the Bering Strait "resets" the system again, and a major production center develops in more stable water downstream in the central Chukchi Sea (Fig. 4), corresponding in area to the "pool" of Shelf/Anadyr water (Fig. 2). Primary production in this center (up to 830 g C m^{-2} y^{-1}) is extremely high and rivals the highest levels observed anywhere else in the World Ocean (Springer & McRoy 1992). This represents the northern terminus of the "Green Belt" (Springer *et al*. 1996). Average production in Anadyr Waters of the Gulf of Anadyr (400 g C m^{-2} y^{-1}), Chirikov Basin (360 g C m^{-2} y^{-1}), and Chukchi Sea (420 g C m^{-2} y^{-1}) far exceeds that of Bering Shelf Water (140 g C m^{-2} y^{-1}) and Alaska Coastal Water (50 g C m^{-2} y^{-1}) as measured in the southeastern Bering Sea. Rather, these high levels of production are typical of upwelling systems (Springer & McRoy 1992) and similar to levels observed in shelf-edge waters in the "Green Belt" of the Bering Sea (e.g., 225-470 g C m^{-2} y^{-1}, Springer *et al*. 1996).

Zooplankton

Zooplankton abundance and distribution in the Bering Strait region are closely related to current and production regimes described above. Patterns of distribution have been established for the entire

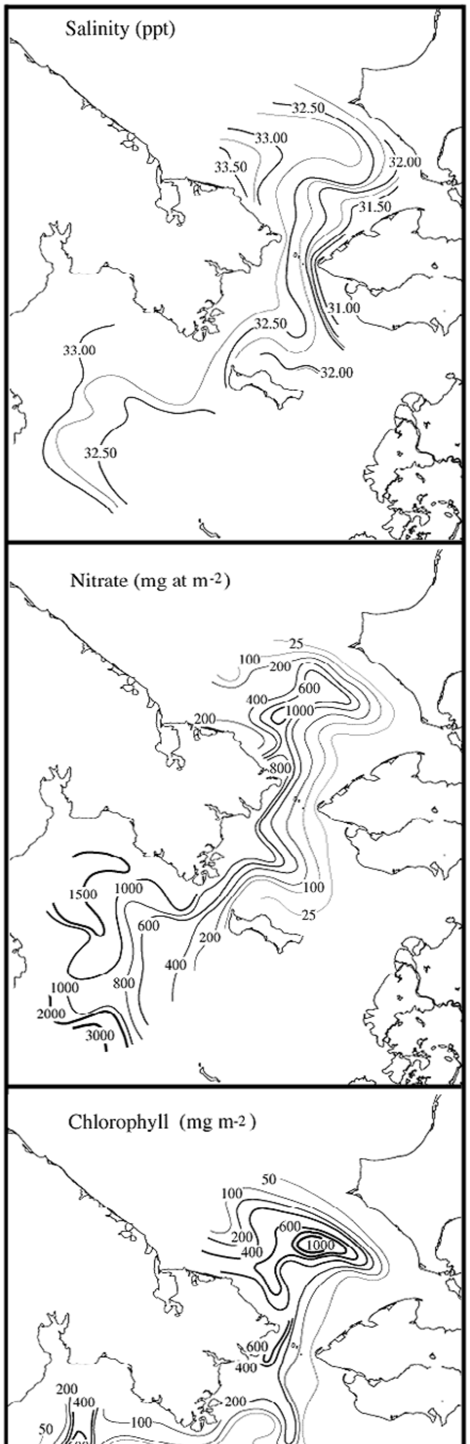

Fig. 4. Areal distribution of bottom salinity (top figure), nitrate (middle) and chlorophyll (bottom) on the Bering-Chukchi shelf (typical example from a cruise on 26 July - 2 September, 1988; from Springer and McRoy 1992). Chlorophyll and nitrate integrated from surface to bottom. Anadyr Water is predominantly above 32.5 ppt.

region by American and Russian investigations conducted over many different months and years, beginning in earnest during the 1950's (Johnson 1956, English 1966, Springer *et al*. 1989, Hunt & Harrison 1990, Piatt *et al*. 1992, Coyle *et al*. 1996 [and references therein]). Among the copepods, the large, oceanic species *Neocalanus cristatus*, *N. plumchru*s, *Eucalanus bungii*, and *Metridia pacifica*, predominate in Anadyr Water (Fig. 5), routinely attaining average densities of 2-4 g_{dry} m^{-2} from spring through late summer. They are replaced in shelf waters mostly by the single large species, *Calanus marshallae*, with typical densities of 0.2-1.2 g_{dry} m^{-2}. Nearshore in Alaska Coastal Water, *C. marshallae* is replaced by a number of small species, particularly *Acartia longiremis*, and *Eurytemora* spp. Biomass densities in coastal water are typically less than 0.5 g_{dry} m^{-2}. Some species are widely distributed in all water types (e.g., *Pseudocalanus* spp., *Oithona similis*), but owing to their smaller sizes, add little to the total standing biomass.

Adult euphausiids are poorly sampled by plankton nets. It is clear from studies of seabird diets (below), however, that in the Chirikov Basin and Bering Strait, euphausiids must be extremely abundant. Perhaps an indicator of adult abundance, euphausiid furcilia (principally *Thysanoessa* spp.) are much more abundant in Anadyr Water (1000s m^{-2}) compared to shelf waters (100s m^{-2}), and are rare in coastal waters (Springer *et al*. 1989). Large pelagic amphipods are also poorly sampled by plankton nets. In the Bering Strait region, *Parathemisto pacifica* is associated with Anadyr Water (Springer *et al*. 1989, Piatt *et al*. 1992).

Patterns of copepod distribution (Fig. 5) reinforce our picture of the oceanographic regime (Fig. 2). Alaska Coastal Water is remarkable for its overall low biomass of zooplankton. *C. marshallae* is a good indicator of Bering Shelf Water, with highest densities found in shelf water northeast of St. Lawrence Island, and east (Fig. 5) of the 32.4 ppt salinity isopleth in the central Chukchi pool (Fig. 2).

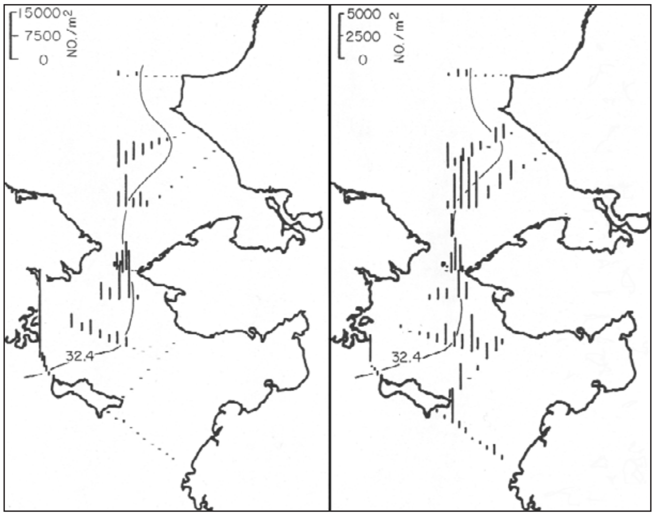

Fig. 5. Areal distribution of oceanic copepods (left panel) and *Calanus marshallae* (right panel) on the Bering-Chukchi shelf (typical example from cruise on 11-26 July, 1986; from Springer *et al*. 1989). Oceanic copepods include combined numbers of *Neocalanus cristatus*, *N. plumchrus*, *Eucalanus bungii*, and *Metridia pacifica*. The line marks the location of the 32.4 ppt salinity isopleth demarcating the interface between Anadyr Water and Bering Shelf Water.

Similarly, oceanic copepods are tightly associated with Anadyr Water below Bering Strait, and are most abundant west of the 32.4 ppt salinity isopleth in the central Chukchi. Spatial segregation of oceanic and shelf copepods in the pool area suggests that Anadyr and Bering Shelf waters retain their identity despite mixing in the Bering Strait. Copepod abundance appears weakly correlated with primary production centers. Highest densities of oceanic copepods were found at production centers on the north side of Anadyr Strait and south of the Diomede islands, but densities in the Chukchi production center were not extraordinary. In contrast, *C. marshallae* densities were highest in the Chukchi center, but otherwise high throughout Chirikov Basin. As most copepods are carried passively by currents, large-scale patterns of distribution may better reflect physical concentration rather than active selection of feeding areas (Sameoto 1982).

Some of the primary production in the Bering-Chukchi system goes toward pelagic secondary production, but most zooplankton biomass is produced in the south and advected northward through the region. Reproduction and growth of most oceanic zooplankton occurs in April-May on the Bering Sea shelf and slope. It takes about 6 weeks for currents to carry this biomass to the northern shelf, producing a peak biomass there in early July. Some species, e.g., *M. pacifica*, reproduce continuously in spring and early summer, resulting in a protracted period of abundance in both regions. Springer *et al*. (1989) estimated that in July 1985, about 35-41 x10^9 g_{dry} d^{-1} of zooplankton were transported through Anadyr Strait, about 1/3 of which were oceanic copepods (i.e., about 10,000 mt d^{-1} of auklet food). Transport rates were strongly correlated with the volume percent of Anadyr Water in Anadyr Strait. Similarly, about 5.6-6.4 x10^9 g_{dry} d^{-1} of zooplankton were transported through Shpanberg Strait, about 1/3 of which were *C. marshallae*. Like *M. pacifica*, the breeding season of *C. marshallae* is protracted, and it is likely that in the 3-7 weeks it takes for water to transit from Shpanberg Strait to the central Chukchi, zooplankton biomass increases from local production and growth.

Theoretically, oceanic zooplankton in Anadyr Water can graze 140-250 mg C m^{-2} d^{-1} of (mainly) diatoms, and at their peak abundance, about 560-1000 mg C m^{-2} d^{-1} (Springer *et al*. 1989). This appears insignificant compared to the average daily diatom production of 1-4 g C m^{-2} d^{-1}, with extremes of 10-16 g C m^{-2} d^{-1}. In shelf waters, *C. marshallae* consumes an average of about 30-50 mg C m^{-2} d^{-1}, whereas during peak abundance, all shelf copepods together consume about 420-575 mg C m^{-2} d^{-1}, approaching the total daily primary production over much of the Bering Shelf (Springer *et al*. 1989).

Pelagic fish

Compared to plankton, there has been little directed study of pelagic fishes in the region (Alverson & Wilimovsky 1966, Wolotira *et al*. 1979, Whitemore & Bergstrom 1983, Naumenko 1996, Brodeur *et al*. 1999), although much can be inferred from diet studies of piscivorous marine birds and mammals (Frost & Lowry 1981, Lowry & Frost 1981, Springer *et al*. 1984, 1987; Piatt *et al*. 1991). Alaska Coastal Water contains a greater diversity of pelagic fishes than shelf waters (Mecklenburg *et al*. 2002). Common forage species in coastal water include (in approximate order of abundance): sandlance *Ammodytes hexapterus*, saffron cod *Eleginus gracilis*, Arctic cod *Boreogadus saida*, herring *Clupea harengus*, and capelin *Mallotus villosus*. Many demersal species occur there also, including a variety of sculpins (Cottidae) and flatfishes (Pleuronectidae). Sand lance and saffron cod are more common south of Bering Strait, whereas Arctic cod are more abundant in the Chukchi Sea.

Capelin and sand lance are found in open waters of the Chukchi, but the abundance of Arctic cod exceeds that of all other fish combined by 1-2 orders of magnitude (Alverson & Wilimovsky 1966). Limited studies indicate a similar trend for the Chirikov Basin and Bering Strait (Frost & Lowry 1981, Springer *et al*. 1987). From St. Lawrence Island to the northeastern Chukchi Sea, excluding inner Norton Sound where saffron cod predominate (Springer *et al*. 1987), Arctic cod are the overwhelmingly dominant prey of piscivorous seabirds (Springer *et al*. 1984, 1987). South and southwest of St. Lawrence Island, Arctic cod are replaced by walleye pollock (*Theragra chalcogramma*) and supplemented by capelin (Hunt *et al*. 1981, Springer *et al*. 1986, Brodeur *et al*. 1999). Bathed in Bering Shelf Water, the environment around St. Lawrence Island is similar in many ways to coastal waters (Springer *et al*. 1987). There are shallow banks, eddies and stratified waters which provide habitat for a variety of fishes including sand lance, saffron cod and capelin. The shallow shelf around the Diomede islands provides similar habitat for pelagic fishes in the Bering Strait. There is little or no information on the fish fauna of Anadyr and Siberian Coastal waters, and mesopelagic fishes dominate in the deep Anadyr basin to the south (Sobolevsky *et al*. 1996).

As observed for zooplankton, there are strong associations between some fish species and water masses (e.g., saffron cod and Alaskan Coastal Water, Springer *et al*. 1987), but others are more cosmopolitan (e.g., Arctic cod, Alverson & Wilimovsky 1966). Strong associations may result from a preference for particular water temperatures or salinities (Brodeur *et al*. 1999, Abookire *et al*. 2000, Robards *et al*. 2002), species-specific food requirements, or to substrate requirements (e.g., sand lance require shallow, sandy substrates; Robards *et al*. 1999). In contrast to zooplankton, fish are more abundant in coastal waters than in open shelf waters. In the Chukchi Sea near Pt. Hope, hydroacoustic surveys indicate an order of magnitude difference between pelagic fish densities in Alaska Coastal Water (0.73 g m^{-3}) and adjacent Bering Shelf Water (0.073 g m^{-3}; Piatt *et al*. 1991). Peak densities inshore (up to 249 g m^{-3}) far exceeded peak densities offshore (up to 80 g m^{-3}). Similarly, Alverson & Wilimovsky (1966) caught fewer Arctic cod (mean ±SE, 58 ±12, n=28) during standardized trawls offshore than on trawls conducted inshore (217 ±144, n=7).

Stratification and stability of the water column may play an important part in determining the relative abundance and distribution of fishes in different water masses (Sogard & Olla 1993, Abookire *et al*. 2000). Pelagic fish may also seek out, or be entrained in, eddies and gyres where plankton are concentrated (Schumacher & Kendall 1991). Hydroacoustic surveys conducted in the Chukchi Sea (Piatt *et al*. 1991) revealed that in shallow, stratified Alaska Coastal Water, pelagic fish densities were relatively high (0.3-3.0 fish m^{-3}). Most fish (and fish schools) were distributed near the bottom or in mid-water. In contrast, plankton scattering layers and pelagic fish were highly dispersed in vertically mixed waters of the frontal zone (ca. 20 km wide) between Alaska Coastal Water and Bering Shelf Water. This transition zone was also characterized by strong lateral sea surface temperature and salinity gradients, and fish abundance was negatively correlated with those property gradients (Piatt *et al*.

1991). Similarly, studies around the Pribilof islands revealed that zooplankton and pelagic fish were concentrated near frontal zones–but mostly in the stratified water side of fronts between stratified shelf waters and mixed coastal waters (Coyle and Cooney 1993, Brodeur *et al*. 1997). Fish and plankton were dispersed and relatively scarce in mixed waters away from the edge of the front.

Further offshore in stratified Bering Shelf Water, relatively low densities (<0.1 fish m^{-3}) of pelagic fish were observed at depths of 20-40 m in association with zooplankton below the thermocline but above a cold (<2ºC) deep layer. Water temperature, and the presence of strong thermoclines, can have a marked influence on the distribution and density of pelagic fish schools in the water column (Coyle and Cooney 1993, Sogard & Olla 1993).

SEABIRD BIOGEOGRAPHY

Piscivore distribution

Seabirds that eat primarily fish, including Common and Thick-billed Murres, guillemots *Cepphus* spp., Horned Puffins *Fratercula corniculata*, Black-legged Kittiwakes *Rissa tridactyla*, *Larus* gulls, and cormorants *Phalacrocorax* spp. (Swartz 1966, Springer *et al*. 1984, 1987, Piatt *et al*. 1991), are concentrated in Alaska Coastal Water, and coastally near islands situated in shelf waters (Fig.6). The largest breeding colonies are found on St. Lawrence Island, near Pt. Hope in the northeast Chukchi Sea, and on the Diomede Islands in the Bering Strait. Small colonies dot the entire Siberian and Alaskan coastlines. Because these seabirds forage near colonies (mostly within 70 km) during summer, major at-sea aggregations coincide spatially with colonies. However, a significant fraction (20-40%) of seabird populations in summer may be comprised of sexually immature birds (1-5 y of age), and failed or post-breeding birds that are not constrained to forage just around colonies (Briggs *et al*. 1987).

The occurrence of large concentrations of piscivorous birds at the sea-surface usually indicates that there are prey schools below (Schneider & Piatt 1986, Cairns & Schneider 1990, Piatt 1990, Mehlum *et al*. 1996). Because the grouped data presents a picture of seabird distribution integrated over summer, and over several years, we conclude that piscivorous seabird distribution (Fig. 6) probably reflects moderate to large-scale temporal and spatial patterns of fish distribution. At the largest scale, the distribution of piscivorous seabirds is defined by where birds do not occur, i.e., in areas of mixed water (Fig. 6). Few seabirds are found in the Coastal-Shelf transition zone, or in the stream of Anadyr and Anadyr-Shelf mixed waters. This is consistent with hydro-acoustic surveys that showed a negative correlation between fish aggregations and turbulent, mixed waters (see above). On a smaller scale, birds are most abundant on the shelves around St. Lawrence and Diomede islands, around headlands in the stream of Alaska Coastal Water, and in a number of eddies in the Chukchi Sea (contrast Figs. 2 and 6). This is consistent with observations that fish are more abundant in Alaska Coastal Water (see above) and that fish aggregate in eddies (Schumacher & Stabeno 1994) and near frontal boundaries around islands (Coyle and Cooney 1993). This pattern of distribution was shown by many individual piscivorous seabird species.

Planktivore distribution

Seabirds that feed primarily on zooplankton, comprising mostly auklets *Aethia* spp. and phalaropes *Phalaropus* spp., have a markedly different distribution from piscivorous seabirds (Fig. 7). Planktivores are for the most part absent from Alaska Coastal Water and coastal-shelf transitional waters. There are few colonies, but they are enormous and positioned strategically in Anadyr and Bering straits to take advantage of the ca. 10 000 mt of zooplankton that are advected daily through the straits (Springer *et al*. 1989). Least and Crested auklets are extremely abundant around the west end of St. Lawrence Island, and also north along the border of the Anadyr Current. Few are found in the downstream plume of Anadyr Water beyond about 100 km from colonies. In Bering Strait, Least Auklets are most abundant to the south in Bering Shelf Water, and Crested Auklets dominate to the west where they straddle the mixed zone of Anadyr-Bering Shelf Water (Piatt *et al*. 1992). The only significant colony of auklets in Alaska Coastal Water is found at King Island (ca. 100 km SSE of Diomedes), but most of these birds over-fly coastal water to forage in Bering Shelf and Anadyr waters to the west (Hunt & Harrison 1990). Planktivores are scarce in the plume downstream of Bering Strait, and most forage within 100 km of the Diomede islands. Large concentrations of planktivores, almost entirely Red Phalaropes *Phalaropus fulicaria*, but also Parakeet Auklets, are found in the central Chukchi Sea. In contrast to piscivores, phalarope

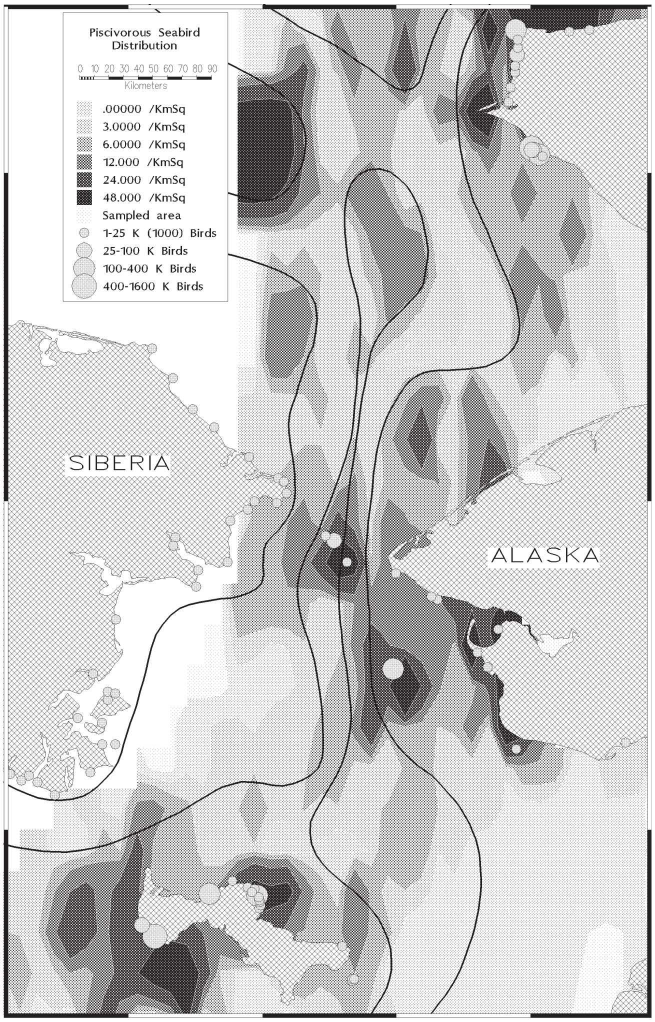

Fig. 6. Areal distribution of piscivorous seabirds on the Bering-Chukchi shelf during summer. "Mixed Water" boundary lines from Fig. 2. See Methods for sources of colony and pelagic distribution data. Note that scales of abundance are the same as in Fig. 7.

aggregations are extended along a southeast to northwest axis, and appear to straddle mixed waters rather than avoid them.

These patterns of distribution are consistent with the biological oceanography of the region (above), and feeding behavior of planktivores. Crested Auklets feed mostly on euphausiids *Thysanoessa* spp. and on large oceanic copepods (*N. plumchrus* and *N. cristatus*), whereas Least Auklets consume mostly oceanic copepods, and some shelf species (*C. marshallae*; Bedard 1969, Springer & Roseaneau 1985, Hunt & Harrison 1990, Piatt *et al.* 1990a, 1992). Auklets exploit waters rich with these plankton, but they are aggregated in only two main areas of the region–even though much of Anadyr-Bering Shelf waters contain a moderate to high abundance of zooplankton throughout (Fig. 5, Springer *et al.* 1989, Coyle *et al.* 1996). Several factors contribute to this restricted distribution. At the largest scale, auklets are constrained by breeding activities (June-September; Piatt *et al.* 1990a) to forage within a fixed distance of colonies (generally about 50 km; Obst *et al.* 1995, Piatt *et al.* 1992). They also appear to avoid areas with high turbulence and mixed waters (Fig. 7). As with piscivores, however, a substantial proportion (20-40%) of auklets are potentially non-breeders (Jones 1992) and may exploit more distant hotspots, if they are suitable. Auklets prefer to forage in stratified Bering Shelf/Anadyr water where pycnoclines (and zooplankton) rise toward the surface in response to topographic features or at the border of upwelling and fronts (Hunt *et al.* 1990, Hunt & Harrison 1990, Hunt *et al.* 1992, Piatt *et al.* 1992). Auklets may also be found in abundance just on the other (mixed) side of the Anadyr-Shelf frontal zone (Haney 1991) or along the border of upwelled waters on the west coast of St. Lawrence Island (Bedard 1969, Springer & Roseneau 1985, Russell *et al.* 1999).

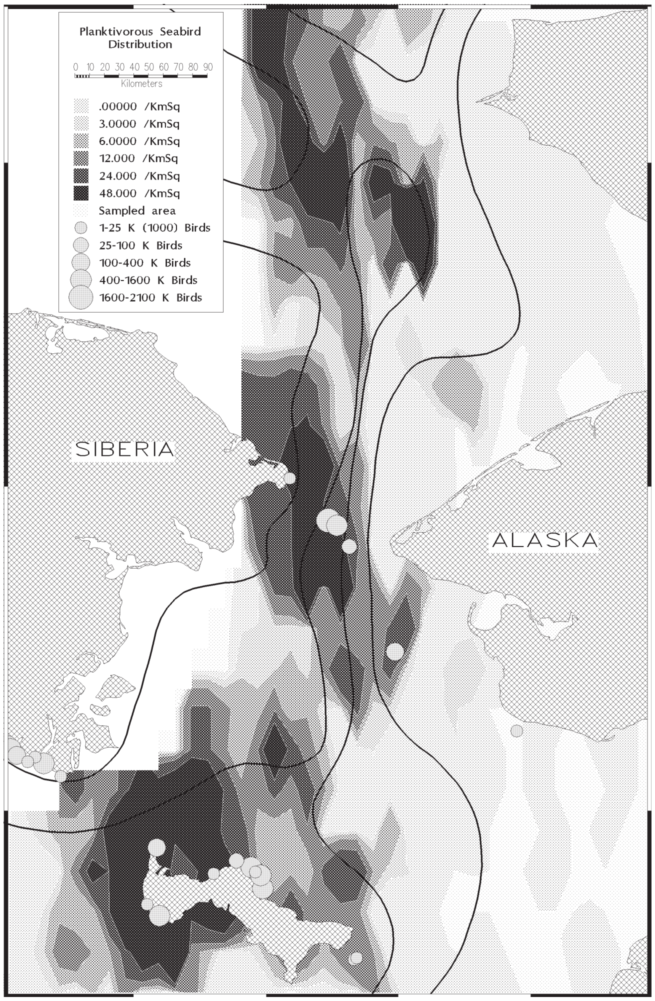

Fig. 7. Areal distribution of planktivorous seabirds on the Bering-Chukchi shelf during summer. "Mixed Water" boundary lines from Fig. 2. See Methods for sources of colony and pelagic distribution data. Note that scales of abundance are the same as in Fig. 6.

On a finer scale, Crested and Least auklets are often segregated spatially, presumably because their preferred prey (euphausiids vs. copepods) are found in different habitats (Piatt *et al.* 1992; Hunt *et al.* 1992). Euphausiids are better able to swim against current flow than copepods, and they may be able to maintain school integrity in frontal and upwelled waters. Often found in layers on the bottom during day, euphausiids may be mechanically concentrated and raised from the bottom by subsurface convergence at the border of upwelling fronts (Simard *et al.* 1986, Schneider *et al.* 1990). Parakeet Auklets are generalist plankton feeders and much more dispersed than Least and Crested auklets. They are most abundant in Shelf/Anadyr waters of Bering Strait, but are also widely distributed in areas of Chirikov Basin and the Chukchi Sea that are little used by Least and Crested auklets (Harrison 1990, Schauer 1991).

Phalaropes (mostly Red Phalaropes) replace auklets as the dominant planktivore in the Chukchi Sea. They eat a wide variety of planktonic prey, including amphipods, copepods, mysids and small euphausiids (Divoky 1984, Brown & Gaskin 1988). Away from the coast, where they may forage in the littoral zone, concentrations of Red Phalaropes are almost always associated with convergent fronts where plankton accumulate in surface slicks (Brown & Gaskin 1988). The vast majority of phalaropes in the Chukchi Sea straddle the mixed water zones marking the convergence of Anadyr Water from the south and Shelf/Anadyr/Coastal waters from the east (Fig. 7).

Omnivore distribution

Short-tailed Shearwaters *Puffinus tenuirostris*, Northern Fulmars *Fulmarus glacialis*, and Tufted Puffins *Fratercula cirrhata* are extremely abundant species in the Aleutians and southern Bering Sea, but relatively few venture far beyond the Bering Strait until August (Divoky 1987). A few small colonies of Tufted Puffins are found in the Chukchi Sea. All these large-bodied species eat a wide variety of prey, including euphausiids, shrimp, squid, and fish (Hunt *et al.* 1981, Schneider *et al.* 1986). Distribution patterns reflect foraging behavior as these species are found in all water masses, and along the Coastal/Shelf transition zone (Piatt *et al.* 1991). Main areas of concentration are in Anadyr Strait (fulmar only), Bering Strait, and the central Chukchi Sea. Fulmars appear to favor Anadyr Water (see also Schauer 1991).

Energetics and carbon flux

For most species that breed in the region, population estimates from colony and at-sea censuses are of a similar order of magnitude (Fig. 8). Least and Crested auklet colony estimates exceed at-sea estimates by 2-4 times, but there are many uncertainties in censusing auklets on land (Piatt *et al.* 1990b, Jones 1992). In all regions, some non-breeding or migratory species (shearwaters, fulmars, phalaropes, etc.) are abundant at sea whereas their colonies are located outside the study area. From a population standpoint, planktivorous auklets are overwhelmingly dominant south of the Bering Strait (Fig. 8). Phalaropes replace auklets as planktivores in the Chukchi Sea, and our estimate is similar to the one million estimated by Divoky (1987) for the region. Murres and Black-legged Kittiwakes are the most abundant piscivorous species in all sub-regions, and are most abundant in the Chukchi Sea. Taking into account the differences in body size among species (Table 1) the relative trophic importance of each species (Fig. 9, upper graph) is quite different from their numerical abundance (Fig. 8). Carbon flux to piscivores rivals that of planktivores south of Bering Strait, and is an order of magnitude greater in the Chukchi Sea. The Bering Strait and the Anadyr Strait (sub-region SLI-CB) support a nearly equal density of auklets. Taking total areas into account, however, it is clear that Anadyr Strait is the nucleus for auklet populations in the region (Fig. 9, lower graph). These estimates do not even account for much (if any) of the huge populations of auklets on the Siberian Coast (Fig. 7), which probably forage in Anadyr Water before it enters Anadyr Strait. Some of the disparity between regional populations may relate to breeding habitat, which is very limited in Bering Strait. Total seasonal (122 d) food consumption is similar in all three sub-regions (29,000 mt; 21,100 mt; 21,900 mt; in SLI-CB, BER-STR, and CHUKCHI, respectively). Whereas half of all food consumed below Bering Strait goes to planktivores (49% of 411 mt d^{-1}), most goes to piscivores (88% of 179 mt d^{-1}) in the Chukchi Sea.

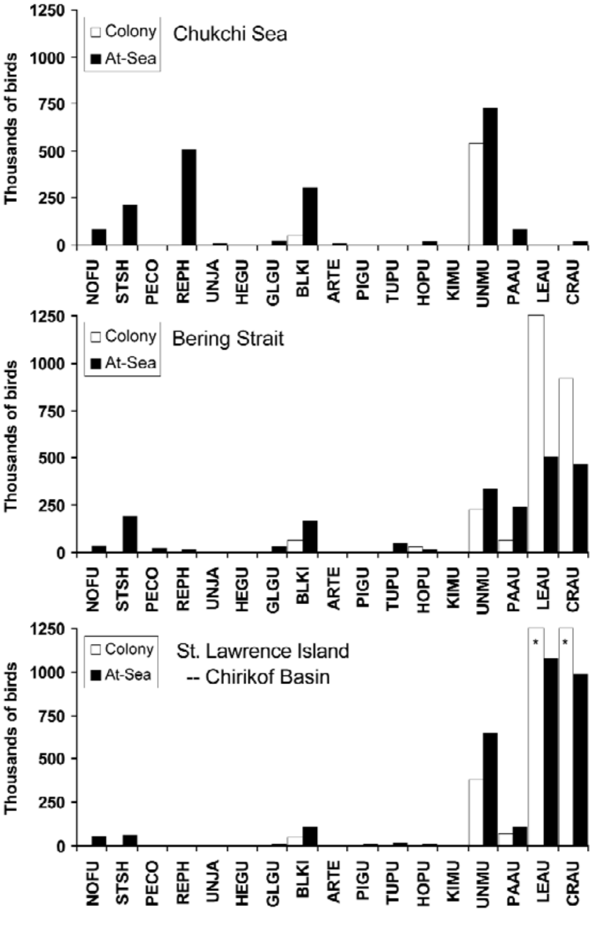

Fig. 8. Total seabird populations in three sub-regions of the Bering-Chukchi shelf. Populations estimated from colony counts (stippled bars) and by extrapolation from at-sea densities (solid black bars). Bars broken by asterisks indicate colony population estimates far in excess of scale (Bering Strait LEAU 2.075 million, Chirikof Basin LEAU 4.125 million, CRAU 3.113 million). Species codes from Table 1. Sub-regions and sources of data described in Methods.

The trophic importance of piscivores is mostly due to the large numbers of murres. In terms of carbon flux, these large-bodied alcids dominate in all shelf seabird communities from central California to the Chukchi Sea (Wiens & Scott 1975, Briggs & Chu 1987, Schneider *et al*. 1987, this study). In contrast to more southern coastal areas where Common Murres predominate, and to the oceanic Aleutian Islands where Thick-billed Murres predominate, Common and Thick-billed Murres are about equally abundant in the Bering Strait-Chukchi region. As noted by Springer *et al*. (1987), this is a direct consequence of having an abundance of both oceanic and shelf foraging environments in the region. Although Thick-billed Murres rely on pelagic fish in shelf habitats, they are also well-adapted for exploiting a wide variety of oceanic prey including euphausiids, amphipods, and squid. Common Murres feed almost exclusively on pelagic schooling fish during summer. Thus, the large mixed-species murre colonies on St. Lawrence Island, in the Bering Strait, and near Pt. Hope are strategically positioned to make full use of both oceanic, shelf and coastal food webs (Springer *et al*. 1987). As expected, the murres overlap in distribution at sea, but Thick-billed Murres are more common in transitional and Bering Shelf/Anadyr waters, and Common Murres are largely restricted to Alaska Coastal Water (Piatt *et al*. 1991, 1992).

With an extremely productive "Green Belt" flowing north, a massive concentration of planktivores, and proximity of coastal and oceanic environments that support both species of murres, the northern Bering-Chukchi system rivals or exceeds most other shelf and upwelling systems that have been studied in terms of carbon

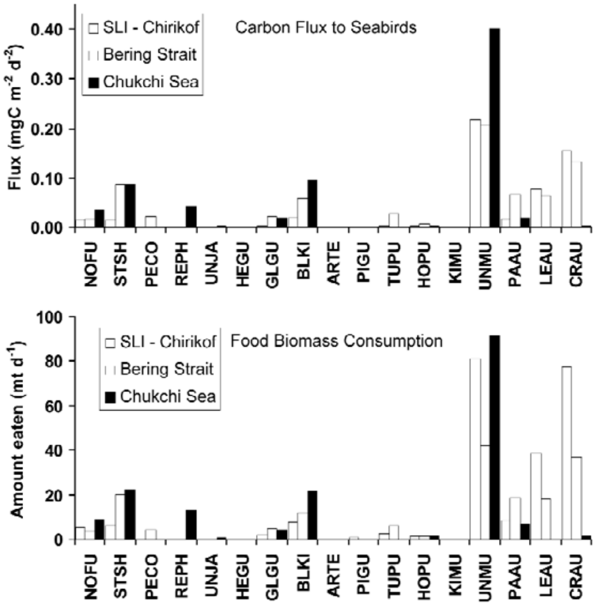

Fig. 9. Carbon flux to seabirds, and estimated biomass consumption of food by seabirds, in three sub-regions of the Bering-Chukchi shelf. Species codes from Table 1. Sub-regions described in Methods.

flux to seabird populations (Table 2). With a high proportion of small-bodied auklets, the standing biomass of seabirds is lower than in most other regions, but this is compensated for by the higher mass-specific metabolic rates of small species.

SUMMARY DISCUSSION

Advection and pelagic food webs

The continental shelf of the northern Bering Sea and southern Chukchi Sea has long been recognized as a region of unusually high marine production – from primary producers (McRoy *et al.* 1972) to seabirds (Fay & Cade 1959, Bedard 1969). The biological richness was paradoxical given the shallow waters of the region and great distance from nutrient sources at the Bering Sea shelf edge. Extensive oceanographic and biological research has resolved this paradox: Advection of oceanic water and biomass from the Bering Sea basin (ca. 800-1200 km away) is primarily responsible for biological richness on the Bering-Chukchi shelf (Sambrotto *et al.* 1984, Springer & Roseneau 1985, Coachman & Shigaev 1992). Extremely high rates of carbon flux to seabirds are clearly a result of this advective regime (Springer *et al.* 1987; this study). Furthermore, advection of oceanic zooplankton accounts for the presence of huge *Aethia* auklet colonies far from upwelling areas typically exploited by these species in the Aleutians and along the Bering Sea shelf edge.

Whereas the advection of nutrients and biomass so far inshore on a continental shelf may be unusual, the process of biomass advection and downstream development on shelf systems is not. For example, a large fraction of pollock larvae produced in Shelikof Strait is advected 300-500 km southwest by prevailing currents along the Alaska Peninsula (Kim & Kendall 1989). Tufted Puffins situated near the beginning of this "conveyor belt" of food eat few of the small pollock larvae, and rely heavily on larger resident pelagic fish like sand lance and capelin (Hatch & Sanger 1992). The proportion and size of juvenile pollock in puffin diets increases dramatically towards the end of the Alaska Peninsula, where juvenile pollock dominate the pelagic fish community. In another advective regime, nutrient enrichment of surface waters through physical mixing in Hudson Strait results in gradual downstream development of plankton, fish (*Gadus morhua*) and seabird biomass in the Labrador Current (Sutcliffe *et al.* 1983). Seabird and fish densities peak off northeast Newfoundland, about 1200 km south of the site of turbulent mixing. Advection also may be an important mechanism for sustaining large seabird colonies situated in the central Canadian Arctic (Cairns & Schneider 1990).

Biogeography of seabirds

At the largest scale (100s-1000s km), the seabird community in the Bering Strait region is physically and biologically structured in a north-south direction by advection of nutrients and biomass from the south and by turbulent mixing at set points along the way. At intermediate scales (10s-100s km) in an east-west direction, seabird distribution is well-defined by water masses, frontal zones and water column stability (Figs. 1-3). In turn, these properties are influenced locally by bottom topography (including islands and headlands), tides, freshwater runoff, surface layering, and wind. Eddies that are created and driven by current flow (barotropic) and density differences (baroclinic) also appear to be common and important structural features in the region (Coachman *et al.* 1975).

In contrast to the strong physical and biological gradients that run from east to west across the Bering Strait region, north-south gradients are generally weaker. For example, all three currents flow south to north, creating similar habitats across the region, and zooplankton species composition, abundance and distribution are similar with respect to those water masses both below and above the Bering Strait (Fig. 5). The same cannot be said, however, for seabirds: planktivores are relatively insignificant consumers above the Bering Strait whereas carbon flux to piscivores nearly doubles in the Chukchi Sea. This appears to result from both physical processes and time required for downstream development of food-webs. We speculate that fish, and therefore piscivores, are less abundant in the central Bering Strait region because upwelling turbulence and rapid currents downstream from Anadyr and Bering straits disrupt zooplankton aggregations and reduce foraging

TABLE 2
Primary production and carbon transfer to seabirds in the Bering Sea and other regions*.

Oceanic Region	Area (km^2)	Primary production ($gC/m^2/y$)	Avian biomass (kg/km^2)	Carbon transfer ($mgC/m^2/d$)
N. Bering-Chukchi	217000	324	15.5	0.65
SLI-Chirikov	99000	360	12.5	0.55
Bering Strait	55000	360	17.1	0.73
Chukchi	62000	420	18.8	0.73
S.E. Bering Shelf	133000	–	18.6	0.49
Inner shelf	39000	75	16.3	0.41
Middle shelf	45000	166	21.2	0.41
Outer shelf	34000	162	36.1	0.68
Slope	14000	225	29.8	0.56
California	163000	130-300	8-20	0.20-0.40
Oregon	22000	300	–	0.86
George's Bank	52000	265-455	–	0.47

* Primary productivity data taken from Springer and McRoy 1993, Springer *et al.* 1996 and following sources. Data on seabird biomass and carbon flux from Wiens and Scott 1975, Schneider *et al.* 1986, 1987, and Briggs and Chu 1987. Southeast Bering Sea biomass and flux calculated from 1980 data in Schneider *et al.* 1986, 1987.

efficiency of fish. In mixed waters adjacent to fronts, zooplankton layers are disrupted by turbulent mixing (Sameoto 1982) and pelagic fish probably avoid well-mixed waters for this reason (Piatt *et al*. 1991). This might seem to contradict a well-established notion that fish and zooplankton are concentrated in frontal areas–but they actually tend to concentrate on the border of the fronts themselves, and most often in stratified waters on the stable side of the front (Coyle and Cooney 1993, Brodeur *et al*. 1997). Well-mixed waters away from frontal boundaries do not provide good foraging habitat for pelagic fish.

Perhaps as importantly, transit time for water between Anadyr and Bering straits is too short (10-20 d in summer) for much growth or development of pelagic fish biomass (Sutcliffe *et al*. 1983) before the system is "reset" again at Bering Strait (Coachman & Shigaev 1992). In the Chukchi Sea, however, currents slow considerably, stratification and eddies develop downstream, and pelagic fish can probably use more fully the plankton biomass advected to them. In contrast, auklets thrive where zooplankton are concentrated on the edge of the turbulent upwelling systems in Anadyr and Bering straits, but no comparable upwelling exists in the Chukchi Sea. Auklets can dive 10-25 m below the surface to capture their prey and they tend to seek out dense plankton layers brought into near-surface waters by upwelling or raised pycnoclines (Hunt *et al*. 1990, 1992). Auklets are replaced by surface-feeding phalaropes in the central Chukchi, which forage on zooplankton concentrated at the surface by convergent fronts (Brown & Gaskin 1988).

Little is known about the overall distribution of fish in the Bering Strait region, but we can assume that the presence of piscivores is a reliable indicator of fish concentrations at many spatial scales (Piatt 1990, Piatt *et al*. 1992, Hunt *et al*. 1990, 1992, Mehlum *et al*. 1996). Piscivores require moderate to high density schools of fish for successful foraging (Piatt 1990), and so their patterns of distribution should also reflect physical mechanisms for concentrating prey of fishes. Some deep-diving (>50 m) piscivores (murres, cormorants) can exploit all of the water column on the Beringian shelf, whereas others (kittiwakes, gulls) must rely on physical or biological mechanisms (e.g., fronts, diel migration) to bring fish to the surface. In any case, the abundance of piscivores in stratified coastal waters and offshore eddies, and their conspicuous absence from mixed and turbulent waters, suggests that these physical factors play a dominant role in structuring piscivorous seabird communities in Beringia.

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REFERENCES

ABOOKIRE, A.A., PIATT, J.F. & ROBARDS, M.D. 2000. Nearshore fish distributions in an Alaskan estuary in relation to stratification, temperature and salinity. *Estuarine and Coastal Shelf Science* 51: 45-59.

ALVERSON, D.L. & WILIMOVSKY, N.J. 1966. Fishery investigations of the southeastern Chukchi Sea. In: Wilimovsky, N.J. & Wolfe, J.N. (Eds.). Environment of the Cape Thompson Region, Alaska Division for Technical Information, U.S. Atomic Energy Commission, Oak Ridge, TN. pp. 843-860

BEDARD, J. L969. Feeding of the Least, Crested, and Parakeet Auklets around St. Lawrence Island, Alaska. *Canadian Journal of Zoology* 47: l025-l050.

BIRT-FRIESEN, V.L., MONTEVECCHI, W.A., CAIRNS, D.K., & MACKO, S.A. 1989. Activity specific metabolic rates of free-living northern gannets and other seabirds. *Ecology* 70: 357-367.

BRIGGS, K.T., TYLER, W.B., LEWIS, D.B., & CARLSON, D.R. 1987. Bird communities at sea off California: 1975 to 1983. *Studies in Avian Biology* No. 11. 74 pp.

BRIGGS, K.T. & CHU, E.W. 1987. Trophic relations and food requirements of California seabirds: updating models of trophic impact. In: J.P. Croxall (Ed.), Seabirds: Feeding Ecology and Role in Marine Ecosystems. Cambridge Univ. Press, Cambridge, England. pp. 279-304

BRODEUR, R.D., WILSON, M.T., NAPP, J.M., STABENO, P.J., & SALO, S. 1997. Distribution of juvenile pollock relative to frontal structure near the Pribilof Islands, Bering Sea. In: Forage Fishes in Marine Ecosystems. Alaska Sea Grant College Report No. 97-01. University of Alaska, Fairbanks. pp. 573-590.

BRODEUR, R.D., WILSON, M.T., & WALTERS, G.E. 1999. Forage fishes in the Bering Sea: Distribution, species associations and biomass trends. In: Loughlin, T.R. & Ohtani, K. (Eds.). Dynamics of the Bering Sea. Univ. of Alaska Sea Grant, AK-SG-99-03, Fairbanks. pp. 509-536.

BROWN, R.G.B., & GASKIN, D.E. 1988. The pelagic ecology of Grey and Red-necked Phalaropes *Phalaropus fulicarius* and *P. lobatus* in the Bay of Fundy, eastern Canada. *Ibis* 130: 234-250.

CAIRNS, D.K., & SCHNEIDER, D.C. 1990. Hot spots in cold water: feeding habitat selection by Thick-billed Murres. *Studies in Avian Biology* 14: 52-60.

COACHMAN, L.R. 1993. On the flow field in the Chirikov Basin. *Continental Shelf Research* 13: 481-508.

COACHMAN, L.R., AAGAARD, K., & TRIPP, R.B. 1975. Bering Strait: the regional physical oceanography. University of Washington Press, Seattle, WA. 172 pp.

COACHMAN, L.R., & AAGAARD, K. 1988. Transports through the Bering Strait: annual and interannual variability. *Journal of Geophysical Research* 93: 15535-15539.

COACHMAN, L.R., & SHIGAEV, V.V. 1992. Northern Bering-Chukchi Sea ecosystem: The physical basis. In: Nagel, P.A. (Ed.). Results of the Third Joint US-USSR Bering and Chukchi Seas Expedition (BERPAC), Summer 1988. U.S. Fish and Wildlife Service, Washington, D.C. pp. 388-398.

COYLE, K.O., & COONEY, R.T. 1993. Water column sound scattering and hydrography around the Pribilof Islands, Bering Sea. *Continental Shelf Research* 13: 803-827.

COYLE, K.O., CHAVTUR, V.G., & PINCHUK, A.I. 1996. Zooplankton of the Bering Sea: A review of Russian-Language Literature. In: Mathisen, O.A. & Coyle, K.O. (Eds.). Ecology of the Bering Sea: a review of Russian literature. Fairbanks, AK, Alaska Sea Grant College Program Rep. 96-01. pp. 97-133.

DIVOKY, G.J. 1984. The pelagic and nearshore birds of the Alaskan Beaufort Sea. U.S. Dep. Commer., NOAA, *OCSEAP Final Report* 23: 397-513.

DIVOKY, G.J. 1987. The distribution and abundance of birds in the eastern Chukchi Sea in late summer and early fall. OCSEAP Final Report, Res. Unit 196. 91 pp.

DUNNING, J.B. 1984. Body weights of 686 species of North American birds. *Western Bird Banding Association Monograph* 1: 1-38.

ELPHICK, C.S., & HUNT, G.L. 1993. Variations in the distributions of marine birds with water masses in the northern Bering Sea. *Condor* 95: 33-44.

ENGLISH, T.S. 1966. Net plankton volumes in the Chukchi Sea. In: Wilimovsky, N.J. & Wolfe, J.N. (Eds.). Environment of the Cape Thompson Region, Alaska Division for Technical Information, U.S. Atomic Energy Commission, Oak Ridge, TN. pp. 809-815.

FAY, F.H. & CADE, T.J. l959. An ecological analysis of the avifauna of St. Lawrence Island, Alaska. *University of California Publications in Zoology* 63: 73-l50.

FLEMING, R.H. & HEGGARTY, D. 1966. Oceanography of the southeast Chukchi Sea. In: Wilimovsky, N.J. & Wolfe, J.N. (Eds.), Environment of the Cape Thompson Region, Alaska Division of Technology and Information, U.S. Atomic Energy Commission, Oak Ridge. pp. 697-754.

FROST, K.J. & L.F. LOWRY. 1981. Trophic importance of some marine gadids in northern Alaska and their body - otolith size relationships. *Fishery Bulletin* 79: 187-192.

GOULD, P.J., & FORSELL, D.J. 1989. Techniques for shipboard surveys of marine birds. U.S. Dept. Interior, Fish and Wildlife Service, Washington D.C., Fish and Wildlife Tech. Rep. 25. 22 pp.

GREBMEIER, C.P. MCROY, C.P., & FEDER, H.M. 1988. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. I. Food supply source and benthic biomass. *Marine Ecology Progress Series* 48: 57-67.

GREBMEIER, C.P., & MCROY, C.P. 1989. Pelagic-benthic coupling on the shelf of the northern Bering and Chukchi Seas. III. Benthic food supply and carbon cycling. *Marine Ecology Progress Series* 53: 79-91.

HANEY, J.C. 1991. Influence of pycnocline topography and water column structure on marine distributions of alcids (Aves: Alcidae) in Anadyr Strait, northern Bering Sea, Alaska. *Marine Biology* 110: 419-435.

HARRISON, N.M. 1990. Gelatinous zooplankton in the diet of the Parakeet Auklet: comparisons with other auklets. *Studies in Avian Biology* 14: 114-124.

HATCH, S.A. & SANGER, G. 1992. Puffins as samplers of juvenile walleye pollock and other forage fish in the Gulf of Alaska. *Marine Ecology Progress Series* 80: 1-14.

HUNT, G.L. & N.M. HARRISON. 1990. Foraging habitat and prey selection by Least Auklets at King Island, Alaska. *Marine Ecology Progress Series* 65:141-150.

HUNT, G.L., JR., BURGESSON, B. & SANGER, G.A. 1981. Feeding ecology of seabirds of the eastern Bering Sea. In: Hood, D.W. & Calder, J.A. (Eds.). The eastern Bering Sea shelf: Oceanography and resources. National Oceanographic and Atmospheric Administration, Juneau, Alaska, pp. 629-648.

HUNT, G.L., HARRISON, N.M., & COONEY, R.T. 1990. The influence of hydrographic structure and prey abundance on foraging of Least Auklets. *Studies in Avian Biology* 14: 7-22.

HUNT, G.L., HARRISON, N.M., & PIATT, J.F. 1993. Aspects of the pelagic biology of planktivorous auklets. In: Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds.), The Status, Ecology and Conservation of Marine Birds in the North Pacific, Canadian Wildlife Service Special Publication, Ottawa. pp. 39-55.

JOHNSON, M.W. 1956. The plankton of the Beaufort and Chukchi sea areas of the Arctic and its relation to the hydrography. Arctic Institute of North America Technical Paper No. 1, Montreal, 33 pp.

JONES, I.L. 1992. Colony attendance of Least Auklets (*Aethia pusilla*) at St. Paul Island, Alaska: implications for population monitoring. Condor 94: 93-100.

KIM, S. & KENDALL, A.W. 1989. Distribution and transport of larval walleye pollock (*Theragra chalcogramma*) in Shelikof Strait, Gulf of Alaska, in relation to water movement. *Conseil International pour l'Exploration de la Mer* 191:127-136.

LOWRY, L.L. & FROST, K.J. 1981. Distribution, growth, and foods of Arctic cod (*Boreogadus saida*) in the Bering, Chukchi, and Beaufort Seas. *Canadian Field Naturalist* 95: 186-191.

MCROY, C.P., GOERING, J.J. & SHIELS, W.S. 1972. Studies of primary production in the eastern Bering Sea. In: Takenouti, A.Y., (Ed.). Biological oceanography of the northern North Pacific Ocean. Motoda Commemorative Vol. 3, Idemitsu Shoten, Tokyo. pp. 199-216.

MEHLUM, F., HUNT, G.L., KLUSEK, Z., DECKER, M.B., & NORDLUND, N. 1996. The importance of prey aggregations to the distribution of Brunnich's Guillemots in Storfjorden, Svalbard. *Polar Biology* 16: 537-547.

NAUMENKO, N.I. 1996. Distribution, biological condition, and abundance of capelin (*Mallotus villosus socialis*) in the Bering Sea. In: Mathisen, O.A. & Coyle, K.O. (Eds.). Ecology of the Bering Sea: a review of Russian literature. Fairbanks, AK, Alaska Sea Grant College Program Rep. 96-01: 237-256.

OBST, B.S., RUSSELL, R.W., HUNT, G.L., JR., EPPLEY, Z.A., & HARRISON, N. M. 1995. Foraging radii and energetics of least auklets (*Aethia pusilla*) breeding on three Bering Sea islands. *Physiological Zoology* 68: 647-672.

OVERLAND, J.E., & ROACH, A.T. 1987. Northward flow in the Bering and Chukchi Seas. *Journal of Geophysical Research* 92: 7097-7105.

PIATT, J.F., ROBERTS, B.D., LIDSTER, W.W., WELLS, J.L., &. HATCH, S.A. 1990a. Effects of human disturbance on breeding success of Least and Crested Auklets at St. Lawrence Island, Alaska. *Auk* 107: 342-350.

PIATT, J.F., ROBERTS, B.D., & HATCH, S.A. 1990b. Colony attendance and population monitoring of Least and Crested Auklets on St. Lawrence Island, Alaska. *Condor* 92: 109-116.

PIATT, J.F. 1990. The aggregative response of Common Murres and Atlantic Puffins to schools of capelin. *Studies in Avian Biology* 14: 36-51.

PIATT, J.F., WELLS, J.L., MACCHARLES, A., & FADELY, B. 1991. The distribution of seabirds and their prey in relation to ocean currents in the southeastern Chukchi Sea. *Canadian Wildlife Service Occasional Papers* 68: 21-31.

PIATT, J.F., PINCHUK, A., KITAISKIY, A., SPRINGER, A.M., AND HATCH, S.A. 1992. Foraging Distribution and feeding ecology of seabirds at the Diomede Islands. Final Rep. for Minerals Management Service (OCS Study MMS 92-041). Anchorage, Alaska. 133 pp.

ROBARDS, M.D., PIATT, J.F., & ROSE, G.A. 1999. Maturation, fecundity and intertidal spawning of Pacific Sand Lance (*Ammodytes hexapterus*) in the northern Gulf of Alaska. *Journal of Fish Biology* 54: 1050-1068.

ROBARDS, M.D., ROSE, G.A., & PIATT, J.F. 2002. Growth and abundance of Pacific sand lance, *Ammodytes hexapterus*, under differing oceanographic regimes. *Environmental Biology of Fishes* 64: 429-441.

RUSSELL, R.W., HARRISION, N.M., & HUNT, GL., Jr. 1999. Foraging at a front: hydrography, zooplankton and avian planktivory in the northern Bering Sea. *Marine Ecology Progress Series* 182: 77-93.

SAMBROTTO, R.N., GOERING, J.J., & MCROY, C.P. 1984. Large yearly production of phytoplankton in western Bering Strait. *Science* 225: 1147-1150.

SAMEOTO, D.D. 1982. Zooplankton and micronekton abundance in acoustic scattering layers on the Nova Scotian slope. *Canadian Journal Fisheries and Aquatic Sciences* 39:760-777.

SCHAUER, A.E.S. 1991. Associations between seabirds and water masses in the northern Bering Sea. In: P.A. Nagel (Ed.). Results of the Third Joint US-USSR Bering and Chukchi Seas Expedition (BERPAC), Summer 1988. U.S. Fish and Wildlife Service, Washington, D.C. pp. 388-398

SCHNEIDER, D.C., & PIATT, J.F. 1986. Scale-dependant aggregation and correlation of seabirds with fish in a coastal environment. *Marine Ecology Progress Series* 32:237-246.

SCHNEIDER, D.C., HUNT, G.L., & HARRISON, N.M.. 1986. Mass and energy transfer to seabirds in the southeastern Bering Sea. *Continental Shelf Research* 5: 241-257.

SCHNEIDER, D.C., HUNT, G.L., & POWERS, K.D. 1987. Energy flux to pelagic birds: a comparison of Bristol Bay (Bering Sea) and Georges Bank (Northwest Atlantic). In: J.P. Croxall (Ed.). Seabirds: Feeding Ecology and Role in Marine Ecosystems. Cambridge Univ. Press, Cambridge, England. pp. 259-277

SCHNEIDER, D.C., HARRISON, N.M., & HUNT, G.L. 1990. Seabird diet at a front near the Pribilof Islands, Alaska. *Studies in Avian Biology* 14: 61-66.

SCHUMACHER, J.D., & STABENO, P.J. 1994.Ubiquitous eddies in the eastern Bering Sea and their coincidence with concentrations in larval pollock. *Fisheries Oceanography*, 3: 182-190.

SIMARD, Y., DE LADURANTAYE, R., & THERRIAULT, J. 1986. Aggregation of euphausiids along a coastal shelf in an upwelling environment. *Marine Ecology Progress Series* 32:203-215.

SOBOLEVSKY, Y.I., SOKOLOVSHAYA, T.G., BALANOV, A.A., & SENCHENKO, I.A. 1996. Distribution and trophic relationships of abundant mesopelagic fishes of the Bering Sea. In: O.A. Mathisen & K.O. Coyle (Eds.). Ecology of the Bering Sea: a review of Russian literature. Fairbanks, AK, Alaska Sea Grant College Program Rep. 96-01: 159-167.

SOGARD, S.M. & OLLA, B.L. 1993. Effects of light, thermoclines, and predator presence on vertical distribution and behavioral interactions of juvenile walleye pollock *Theragra chalcogramma* Pallas. *Journal of Experimental Marine Biology and Ecology*. 167: 179-195.

SOWLS, A. L., HATCH, S. A., LENSINK, C. J. 1978. Catalog of Alaskan seabird colonies. U.S. Dep. Interior, Fish and Wildl. Serv., FWS/OBS-78/78

SPRINGER, A.M., ROSENEAU, D.G., MURPHY, E.C., & SPRINGER, M.I. l984. Environmental controls of marine food webs: food habits of seabirds in the eastern Chukchi Sea. *Canadian Journal Fisheries and Aquatic Sciences* 41: 1202-1215.

SPRINGER, A.M., & ROSENEAU, D.G. 1985. Copepod-based food webs: auklets and oceanography in the Bering Sea. *Marine Ecology Progress Series* 21:229-237.

SPRINGER, A.M., ROSENEAU, D.G., LLOYD, D.S., MCROY, C.P., & MURPHY, E.C. 1986. Seabird responses to fluctuating prey abundance in the eastern Bering Sea. *Marine Ecology Progress Series* 32: 1-12.

SPRINGER, A.M., MURPHY, E.C., ROSENEAU, D.G., MCROY, C.P., & COOPER, B.A. 1987. The paradox of pelagic food webs in the northern Bering Sea - I. Seabird food habits. *Continental Shelf Research* 7: 895-9ll.

SPRINGER, A.M., MCROY, C.P., & TURCO, K.R. 1989. The paradox of pelagic food webs in the northern Bering Sea - II. Zooplankton communities. *Continental Shelf Research* 9:359-386.

SPRINGER, A.M. & MCROY, C.P. 1993. The paradox of pelagic food webs in the northern Bering Sea - III. Patterns of primary production. *Continental Shelf Research* 13: 575-599.

SPRINGER, A.M., MCROY, C.P., & FLINT, M.L. 1996. The Bering Sea Green Belt: shelf edge processes and ecosystem production. *Fisheries Oceanography* 5: 205-223.

SUTCLIFFE, W.H., LOUCKS, R.H., DRINKWATER, K.F., & COOTE, A.R. 1983. Nutrient flux onto the Labrador Shelf from Hudson Strait and its biological consequences. *Canadian Journal Fisheries and Aquatic Sciences* 40: 1692-1701.

SWARTZ, L.G. 1966. Sea-cliff birds. In: Wilimovsky, N.J. & Wolfe, J.N. (Eds.). Environment of the Cape Thompson region, Alaska. U.S. Atomic Energy Commission, Oak Ridge, TN, pp. 611-678.

WIENS, J.A., & SCOTT, J.M.. 1975. Model estimation of energy flow in Oregon coastal bird populations. *Condor* 77: 439-452.

WOLOTIRA, R.J., SAMPLE, T.M., & MORIN, M. 1979. Baseline studies of fish and shellfish resources of Norton Sound and the southeastern Chukchi Sea. Environ. Assess. Alaskan Cont. Shelf, Final Rep. Prin. Invest. Vol. 6: 258-572.

GALÁPAGOS ISLANDS TO BRITISH COLUMBIA: SEABIRD COMMUNITIES ALONG A 9000 KM TRANSECT FROM THE TROPICAL TO THE SUBARCTIC EASTERN PACIFIC OCEAN

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SUMMARY

SMITH, J.L. & HYRENBACH, K.D. Galápagos Islands to British Columbia: seabird communities along a 9000 km transect from the tropical to the subarctic eastern Pacific Ocean. *Marine Ornithology* 31: 155-166.

Studies of seabird biogeography show that species distributions are related to wind conditions, the extent of water masses and ocean productivity patterns over scales of 1000s km. We document changes in the composition of marine bird communities in relation to remotely-sensed water mass properties and wind conditions along a 9,000 km transect across the northeastern Pacific Ocean during a 47 day (20 April – 5 June 1999) cruise from the Galápagos Islands, Ecuador (0º 43.4' S; 90º 32.7' W) to British Columbia, Canada (48º 49.5' N; 125º 8.22' W). We characterized three different marine bird communities along the transect: tropical (booby - tropicbird - frigatebird), subarctic (alcid - fulmar) and a widely-distributed cosmopolitan assemblage dominated by tubenoses (Procellariiformes) (albatrosses, shearwaters, and storm-petrels). These communities inhabit different oceanic regions characterized by distinct water mass properties (e.g., sea surface temperature, chlorophyll concentration). The shift from the tropical to the subarctic community occurred rather abruptly at approximately 20º N. In addition to the latitudinal gradient in community composition, we noted a change in the relative importance of different feeding guilds at higher latitudes, namely an increase in the relative abundance of diving seabirds and a concurrent decrease in plunge-divers. These results support previous evidence of spatial segregation of marine bird species and feeding guilds across the North Pacific Ocean. Our study also provided an opportunity to survey pelagic seabird distributions within a poorly studied region during an anomalous year. In 1999, wind patterns along the entire cruise deviated from the long-term average, with a virtual collapse of the trade winds typically found below 15° N. Moreover, cold-water conditions, associated with a strong La Niña event were apparent throughout the survey track. This paper highlights the continued importance of ocean exploration and standardized time series for the study of seabird biogeography. We encourage other investigators to retrace this survey track in the future.

Keywords: biogeography, community structure, seabird assemblages, fronts, water masses, Galápagos, North Pacific Ocean

RESUMEN

Previos estudios biogeográficos han revelado que las distributiones de las aves marinas estan relacionadas con los patrones de viento, la distribución de masas de agua y la productividad a grandes escalas espaciales (1000s km). En este artículo, relacionamos la composición de las comunidades de aves marinas con las propiedades de las masas de agua, a lo largo de un transecto de 9,000 km a través del Pacifico oriental, desde las Islas Galápagos, Ecuador (0º 43.4' S; 90º 32.7' W) a la Columbia Británica, Canada (48º 49.5' N; 125º 8.22' W).

Hemos documentado tres tipos diferentes de comunidades a lo largo de este transecto: una tropical (pajaro bobo - rabijunco - fregata), una subárctica (alcidos - fulmares) y otra compuesta de especies cosmopolitas dominada por los petreles (albatroses, paiños y pardelas). Estas comunidades habitan regions distintas del Oceano Pacífico, characterizadas por propiedades diferentes (e.g., temperatura en superficie, concentración de clorofila). En particular, recalcamos un cambio drástico de especies a una latitud de 20º N, con una abrupta transición de la comunidad tropical a la subárctica. Además, documentamos un cambio en la incidencia de distintos gremios de forrajeo. A medida que aumentó la latitud, incrementó la proporción de pajaros que se sumergen para pescar y disminuyeron las especies que se zanbullen desde el aire. Estos resultados refuerzan previa evidencia de la segregación espacial de distintas especies y gremios en el Pacífico Norte. Además, nuestro estudio proporcionó una gran oportunidad para estudiar las distribuciones de aves pelágicas en una zone poco estudiada con anterioridad, y durante un año de condiciones oceanográficas extraordinarias. En 1999, los patrones atmosféricos fueron anómalos, con un colapso de los vientos aliseos que normalmente se encuentran al sur de la latitud 15° N. Además, la temperatura del mar fue muy baja, debido al desarrollo de un fuerte La Niña. Este artículo subraya la importancia de la exploración de los oceanos y la necesidad de observaciones estandarizadas para el estudio de la biogeografía de las aves marinas. En particular, es necesario llevar a cabo cruceros en zonas poco estudiadas por los ornitólogos para aumentar nuestros conocimientos de las distribuciones de las especies. Sin embargo, aunque un solo crucero puede aportar interesantes resultados, repetidos muestreos estandarizados son esenciales para comprender como la avifauna marina responde a la variabilidad temporal en las condiciones oceanográficas. Por lo tanto, incitamos a nuestros colegas a que repitan este trayecto en el futuro.

INTRODUCTION

The distributions of nektonic predators, including seabirds, marine mammals, and large predatory fishes, reflect the same large-scale oceanographic domains and current systems that influence ocean productivity and plankton biogeography (Fager & McGowan 1963, Gould & Piatt 1993, McKinnell & Waddell 1993, Brodeur *et al.* 1999, Springer *et al.* 1999). In particular, studies of marine bird communities over scales of >1000 km have revealed that species with different foraging methods, wing morphologies, and diving capabilities preferentially inhabit specific regions of the world's ocean (Ashmole 1971, Ainley 1977, Ballance *et al.* 1997). This ecological segregation suggests that distinct assemblages are adapted to exploit specific water masses (Schneider *et al.* 1987, Wahl *et al.* 1989, Spear & Ainley 1998). In the North Pacific Ocean, diving seabirds preferentially inhabit highly productive areas, characterized by cool ocean temperatures and high chlorophyll concentrations. Conversely, tropical and subtropical waters of lower productivity typically support species that feed at the surface or pursue prey by plunge diving (Ainley 1977, Wahl *et al.* 1989, Gould & Piatt 1993, Ballance *et al.* 1997).

The North Pacific is characterized by strong spatial gradients and substantial temporal variability in atmospheric and hydrographic properties, including wind and ocean productivity patterns (Venrick *et al.* 1987, Polovina *et al.* 1994, Schwing *et al.* 2000), which influence the dispersion of highly migratory marine predators and their prey (Polovina 1996, Lehodey *et al.* 1997, Hyrenbach & Veit 2003). In particular, two large-scale spatial gradients in ocean productivity, prey biomass, and seabird abundance are apparent: a latitudinal (North – South) and an onshore-offshore (East – West) ecotone. The highest ocean productivity levels and standing stocks of marine seabirds and their prey occur in subpolar coastal areas, while lower productivity and standing stocks are found in pelagic waters at lower latitudes (Gould & Piatt 1993, Vinogradov *et al.* 1997, Shimoto *et al.* 1998).

In addition to these spatial gradients, specific water masses, large-scale atmospheric pressure systems, and ocean productivity patterns undergo substantial variability in extent, location, and intensity at inter-annual and longer temporal scales (Venrick *et al.* 1987, Mantua *et al.* 1997, Chavez *et al.* 2003). These year-to-year shifts are particularly strong in the eastern Pacific Ocean, where periodic changes in sea surface temperature and primary productivity are associated with variability in the El Niño Southern Oscillation (ENSO) (Barber & Chavez 1986, Chavez *et al.* 2002). Approximately eight months prior to the observations described in this paper, one of the strongest La Niña events in several decades developed in the NE Pacific. By the start of this cruise, large masses of cool water extended across the Pacific Ocean, from 20-60º N, and from the West Coast of North America to 130º W (Hayward *et al.*1999, Bograd *et al.*2000, Schwing *et al.* 2000).

This paper documents seabird distributions and community structure along a 9,000 km transect across the northeast Pacific Ocean, extending from tropical to subarctic latitudes. We assess whether seabird species are closely or loosely associated into groups of recurrent species, and quantify their oceanographic habitats (e.g., water depth, ocean temperature, chlorophyll concentration). This study provides a snapshot of marine bird dispersion and oceanic habitats during a single cruise. To better interpret this static perspective in the context of dynamic atmospheric and oceanographic processes, we discuss the environmental conditions during the spring of 1999 in relation to the climate of the northeast Pacific Ocean.

METHODS

Seabird observations

Data were collected during a 47 d (20 April - 5 June 1999) cruise of the 13-m vessel S.V. Minke I (cutter rig) from the Galápagos Islands, Ecuador (00.723° S; 90.545° W) to Bamfield, British Columbia, Canada (48.825° N; 125.137° W) (Fig. 1). The survey track followed a published route (three waypoints) that guides offshore sailors from the Galápagos Islands to British Columbia: (1) 2° N; 105° W, (2) 20° N; 125° W, and (3) 40° N; 135° W (Cornell 1992). Most of the track was completed under sail, tacking across the wind as required by local conditions. The actual distance traveled between successive noon-time locations and the daily sailing speeds were both influenced by the changing wind

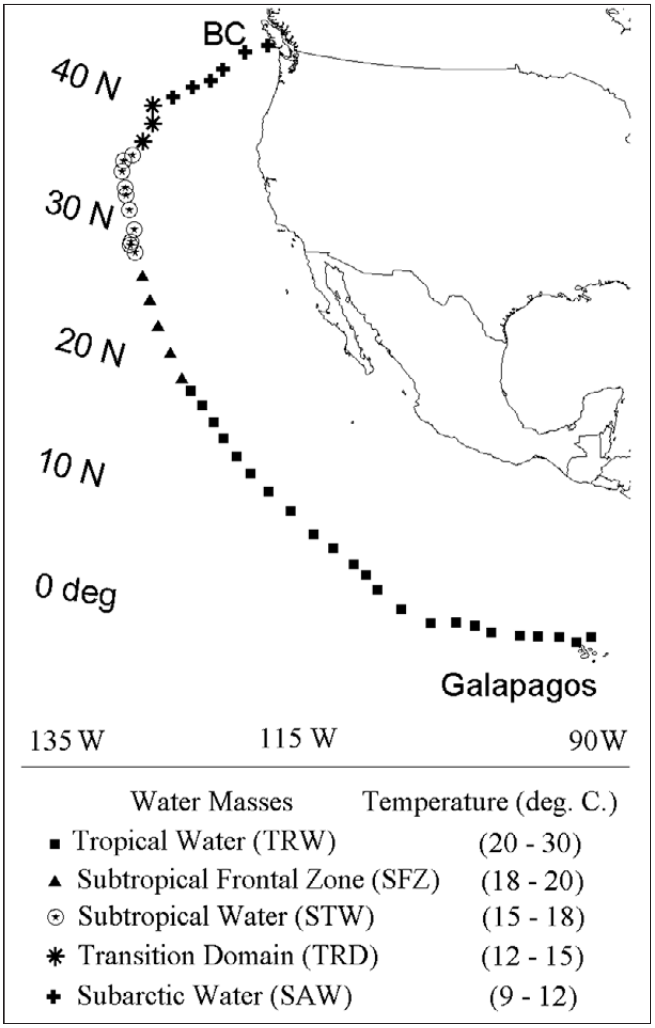

Fig. 1. The survey track of 47 daily noon locations, coded on the basis of distinct water masses, defined in terms of the sea surface temperature.

conditions (mean daily distance: 183.3 ± 59.0 (SD) km, range: 33.3 to 59.0 km, n: 47; mean speed 7.8 ± 2.5 km hr^{-1}, range 1.4 km hr^{-1} to 12.4 km hr^{-1}, n: 47). The total survey line spanned over 9 000 km, while the linear track linking the 47 daily noon locations accounted for 5 600 km.

One of us (JS) surveyed marine birds from the cockpit, (approximately 2 m above the ocean surface) during daylight hours following a rotating schedule of 3-h watches and 6-h resting periods. Over the course of seven weeks, 240 hours were dedicated to seabird observations with an additional 160 hours done opportunistically during rest periods. Seabird observations ceased whenever visibility compromised the ability to detect and identify the birds (e.g., fog, high winds).

All seabirds sighted within 250 m of either side of the vessel were identified to the lowest taxonomic level possible, with the horizontal distance estimated by eye. Behaviour (e.g., sitting, flying, feeding), age class and gender were recorded for each sighting. Ship-following birds were recorded when they were first encountered, and ignored thereafter. Floating marine garbage and the neustonic invertebrate *Velella velella* were also recorded to examine their co-occurrence with convergence zones and foraging pelagic birds. The daily, local noon-time position of the vessel and the location of most seabird sightings were recorded using the onboard global positioning system (GPS).

Due to variable wind conditions and cruising speeds throughout the entire survey, each 3-h sampling period covered a different length of trackline. The estimation of standardized marine bird densities (number km^{-2}) was not possible due to the variability in the vessel's cruising speed, the irregular spacing and length of the survey bins, and the inability to quantify the movement of flying birds relative to that of the vessel (Tasker *et al*. 1984, Spear *et al*. 1992, Garthe & Hüppop 1999). However, the data were used to analyse marine bird community structure and habitat associations on the basis of the relative abundance of different taxa within specific oceanic regions and water masses. For each daily survey, we calculated the numerical importance of each taxon by dividing the number of individuals belonging to each species by the total number of birds sighted. Thus, our dataset expressed the daily proportional contribution of the different species to the total number of birds sighted along the survey track.

Seabird community structure

In addition to presenting the number and identity of the species recorded, we used multivariate statistics to determine whether certain species co-occurred in space and time, and whether distinct seabird assemblages inhabited different water masses. We combined the several 3-h watches completed each day and considered the 47 daily totals as independent samples. Thus, our community-level analyses considered 47 daily observations and the concurrent environmental conditions measured at each of the local noon-time positions.

We were interested in whether the avifauna observed on this cruise consisted of fixed communities or chance associations. If assemblages were predictable, then species that use the same area of the ocean would be significantly associated with each other. We used recurrent group analysis (RGA) to quantify the degree of co-occurrence between species in time and space (Fager & McGowan 1963, Veit 1995). This technique, originally proposed by Fager (1957) and subsequently modified by Venrick (1982), identifies objective groups of recurrent species defined by the strength of their association (∀):

$$\forall = [J\ (Na\ Nb)^{-1/2}] - [1/2\ (Nb)^{1/2}]$$

where J is the number of joint occurrences; Na is the total number of occurrences of species A; Nb is the total number of occurrences of species B; and species are coded such that Na ≤ Nb. The first term of the equation above ranges from 0 to 1, and quantifies the degree of co-occurrence. The second term accounts for disparities in sample sizes (number of species occurrences) for different species pairs, and is always a number smaller than 1 (Fager 1957, Fager & McGowan 1963). The association value (∀) provides a quantitative metric of species association. Investigators frequently select a "threshold" ∀ value and consider higher indices indicative of a "positive" inter-specific association, with all such species in the recurrent group forming a distinct community (Fager & McGowan 1963, Venrick 1982).

We used the empirically-derived distribution of observed ∀ values to identify those species that co-occurred more than would be expected by chance. We restricted our analysis to the 15 taxa that were sighted in more than 5% of the 47 survey days. We included unidentified frigatebirds because these were likely either Great Frigatebirds *Fregata minor* and Magnificent Frigatebirds *F. magnificens* (Harrison 1985) but excluded unidentified storm-petrels and shearwaters because these could include many different species with disparate biogeographic affinities. We computed the ∀ value for each of the possible 120 pair-wise comparisons, and defined the threshold value of "positive association" as the mean (0.023) plus one standard deviation (0.233) of the observed, pair-wise ∀ values.

We organized the positively associated species into the fewest number of recurrent groups by assembling the largest possible group first and then all smaller, subsequent ones. Group membership required that a species had a positive affinity with all other group members, while taxa not associated with all the members of an already existing group were linked as "associates". The links between recurrent groups and associate species were quantified using the proportion of group members that had a positive association with the "associate" species, ranging from 0 to 1 (Venrick 1982).

Environmental data

We characterized habitats using six variables: (1) sea-surface temperature (° C), (2) chlorophyll concentration (mg m^{-3}), (3) wind speed (m s^{-1}), (4) ocean depth (m), (5) latitude (° N), and (6) longitude (° W) (Table 1). Ocean temperature and chlorophyll concentration are useful proxies of water mass distributions and ocean productivity domains (Sverdrup *et al*. 1942, Longhurst 1998), and have been previously used to characterize the oceanographic habitats of North Pacific seabirds (Wahl *et al*. 1989, Hyrenbach *et al*. 2002). Additionally, wind speed is an important determinant of the composition of marine bird communities, since regions of high and low wind are preferentially inhabited by species with different wing morphologies, and prevailing wind conditions likely influence seabird migration routes (Spear & Ainley 1998, 1999). In particular, because wind speed and direction influence the ranging and activity patterns of marine birds, changing wind conditions may alter the number and identity of the birds sighted within a given area (Weimerskirch *et al*. 2000). Similarly, water depth shapes seabird distributions, as indicated by the disparate communities that inhabit distinct bathymetric domains (e.g., shallow continental shelves versus deeper pelagic waters offshore) (Schneider *et al*. 1986).

In addition to these environmental variables, the distance to breeding colonies is an important determinant of pelagic bird distributions and community structure (Stahl *et al*. 1985, Veit 1995). As the cruise passed within 1000 km of several large seabird colonies, (e.g., Galápagos Islands, Clipperton Islands, and Isla de Revillagigedo), we used the location along the survey track to account for potential species range limits.

We used weekly averages of filtered sea surface temperature (SST) imagery from the Advanced Very High Resolution Radiometer (AVHRR), with a spatial resolution of 1 degree latitude x longitude, to quantify ocean temperatures along the survey track (Reynolds & Smith 1994). These data are available at the Pacific Marine Environmental Laboratory web-site (www.ferret.noaa.gov/fbin/climate_server). Global comparisons have revealed that AVHRR SST measurements are 0.3-0.4° C lower than concurrent vessel-based observations, with cross-correlations ranging between + 0.3 and + 0.7 (McClain *et al*. 1985).

Chlorophyll concentrations were derived from Sea-viewing Wide Field-of-view Sensor (SeaWiFS) eight-day composites, with a spatial resolution of 9 km (seawifs.gsfc.nasa.gov/ SEAWIFS.html). Within the range of 0.05-50 mg m^{-3}, SeaWiFS estimates are within 35% of in-situ chlorophyll a concentrations (Hooker & McClain 2000), with the greatest discrepancies in waters between 1-10 mg m^{-3} (Kahru & Mitchell 1999). We discarded unreasonably high chlorophyll a concentrations beyond the range of SeaWiFS validation (> 50 mg m^{-3}) (Hooker & McClain 2000). Because the spatial resolution of the chlorophyll data was finer than the temperature imagery, we aggregated the SeaWiFS images into 100 x 100 km grids, comparable to the resolution of the temperature data (1 degree latitude x longitude). We calculated the median chlorophyll concentration of the 121 (11 x 11) pixels within each grid cell, and used this value for the subsequent habitat analyses.

We used 12-h averages of surface-wind magnitude data from the Fleet Numerical Oceanography Center (FNMOC), with a spatial resolution of 1° x 1° grids (Clancy 1992). These observations are available twice daily (at 0 and 12 hours) at the Pacific Fisheries Environmental Laboratory web-site (las.pfeg.noaa.gov/las/main.pl). To match the timing of the concurrent day-time seabird observations, we used the 47 daily noon wind speed values in our analysis.

Finally, we obtained bathymetric data from NOAA's National Geophysical Data Center ETOPO 5-minute grid elevation dataset (NGDC 1998), and aggregated these fine-scale data into 1° x 1° grids. We calculated the average depth of the 144 (12 x 12) values within each grid cell, and used these data to quantify ocean depth along the survey track.

Analysis of seabird-habitat associations

In addition to the recurrent group analysis, we used non-metric multi-dimensional scaling (NMDS) to quantify the association between seabird distributions and the environmental variables described above. NMDS is a non-parametric ordination technique and does not impose any assumptions on the shape of the habitat-wildlife relationships, the number of explanatory variables defining the species ranges, or the degree of association required to define significant species clusters. Instead, NMDS plots each species on a multi-dimensional space defined by several habitat axes, which represent combinations of the environmental variables used in the analysis. This technique plots species along a multi-variable continuum. Thus, taxa with similar distributions are plotted closer together than those with different distributions (Kenkel & Orloci 1986, Brodeur *et al*. 1999). We used the PC ORD statistical software to perform the NMDS analysis and to create the plots of species distributions (McCune & Mefford 1999).

Segregation across water masses

We evaluated the correlations between the six variables used to characterize seabird habitats, measured at the 47 daily noon-time locations. We found that eight of the 15 possible pair-wise comparisons were significant. In addition to latitudinal ecotones (wind speed and ocean temperature) and longitudinal gradients (ocean depth, wind speed, and ocean temperature), these cross-correlations revealed that shallow, shelf-slope waters supported higher chlorophyll concentrations than deeper pelagic waters, and that higher wind speeds were associated with colder areas of the ocean (Table 1). Because many of the habitat variables were cross-correlated, we focused on the significance of sea surface temperature as a determinant of seabird community structure. This

TABLE 1

Summary of cross-correlations between the six environmental variables used to characterize oceanographic habitats, measured at 47 daily noon-time locations: sea surface temperature (SST), wind speed (WSP), depth (DPH), latitude (LAT), longitude (LON), and chlorophyll concentration (CHL). For each pair-wise combination, the matrix below shows the sign and the magnitude of the Pearson correlation coefficient, and the associated significance level. The bold font denotes significant results.

p-value

	SST	WSP	DPH	LAT	LON	CHL
SST	-	$p < 0.001$	$p > 0.50$	$p < 0.001$	$p < 0.001$	$0.20 < p < 0.10$
WSP	- 0.544	-	$0.50 < p < 0.25$	$p < 0.001$	$p < 0.001$	$p > 0.50$
DPH	- 0.067	+ 0.113	-	$0.20 < p < 0.10$	$p < 0.001$	$p < 0.001$
LAT	- 0.949	+ 0.536	+ 0.208	-	$p < 0.001$	$0.20 < p < 0.10$
LON	+ 0.768	- 0.536	- 0.573	- 0.895	-	$p > 0.50$
CHL	- 0.216	+ 0.079	- 0.660	+ 0.212	+ 0.040	-

r-coefficient

approach facilitated the study of marine bird distributions and community structure with respect to distinct water masses (Wahl *et al*. 1989, Gould & Piatt 1993, Hyrenbach *et al*. 2002).

We characterized the seabird assemblages within six distinct water masses, defined on the basis of remotely-sensed sea surface temperature: the Tropical Water Mass (TRW) (SST > 20º C), the Subtropical Frontal Zone (STF) (SST: 20-18.01º C), the Subtropical or Central Pacific Water Mass (STW) (SST: 18-15.01º C), the Transition Domain (TRD: 15-12.01º C), and Subarctic waters (SAW) (12-9º C) (Lynn 1986, Roden 1991). We graphically contrasted the relative abundance of different types of seabirds within these five water masses. Additionally, we computed the proportion of divers, plunge-divers, and surface-foraging birds in each temperature range, and used the G statistic to test for significant differences in the composition of the avifauna (Zar 1984). We hypothesized that plunge-diving species would be numerically-dominant in warm tropical waters, while divers would be disproportionately more numerous in cool, subarctic waters (Ainley 1977, Wahl *et al*. 1989).

RESULTS

Seabird observations

We recorded 974 seabirds (814 identified individuals belonging to 32 species, 11 families, and three orders) during the 47 day survey (Tables 2, 3). The Sooty Shearwater *Puffinus griseus* and the Black-footed Albatross *Phoebastria nigripes* accounted for 28% of all identified birds (17 and 11%, respectively); all other species were each less than 10% of birds sighted. Most species (63.5%) were sighted more than once, with five taxa (Black-footed Albatross, Leach's Storm-petrel *Oceanodroma leucorhoa*, Sooty Shearwater, Masked Booby *Sula dactylatra*, and Northern Fulmar *Fulmarus glacialis*) observed during more than 10 survey days (Table 2).

Recurrent group analysis

Twenty-six of the 120 pair-wise comparisons involving the "common" taxa (species observed in at least three daily samples) yielded ∀ values larger than our assigned threshold (0.257). These fifteen species formed four recurrent groups characteristic of

TABLE 2
Species list, foraging guilds, and relative occurrence and abundance of seabirds observed during 47 day cruise in northeast Pacific, 20 April - 5 June 1999.

Species Name	Genus and species	Code	Guild	% Days	% Birds
Black-footed Albatross	*Phoebastria nigripes*	BFAL	surface	44.7	10.8
Short-tailed Albatross	*Phoebastria albatrus*	STAL	surface	2.1	0.1
Northern Fulmar	*Fulmarus glacialis*	NOFU	surface	21.3	6.5
Pink-footed Shearwater	*Puffinus creatopus*	PFSH	dive	6.4	1.3
Flesh-footed Shearwater	*Puffinus carneipes*	FFSH	dive	4.3	1.1
Wedge-tailed Shearwater	*Puffinus pacificus*	WTSH	dive	4.3	0.4
Sooty Shearwater	*Puffinus griseus*	SOSH	dive	34.0	16.8
Shearwater species	*Puffinus* spp.	SHEA	dive	31.9	4.8
Audubon's Shearwater	*Puffinus lherminieri*	AUSH	dive	4.3	0.2
Black Petrel	*Procellaria parkinsoni*	BLPE	surface	4.3	2.2
Galapagos Petrel	*Pterodroma phaeopygia*	DRPE	surface	2.1	0.1
Wilson's Storm-petrel	*Oceanites oceanicus*	WISP	surface	12.8	4.3
Fork-tailed Storm-petrel	*Oceanodroma furcata*	FTSP	surface	10.6	3.8
Leach's Storm-petrel	*Oceanodroma leucorhoa*	LESP	surface	34.0	6.3
Madeiran Storm-petrel	*Oceanodroma castro*	MASP	surface	6.4	0.3
Black Storm-petrel	*Oceanodroma melania*	BLSP	surface	2.1	0.1
Wedge-rumped Storm-petrel	*Oceanodrama tethys*	WRSP	surface	10.6	2.5
Elliott's Storm-petrel	*Oceanites gracilis gracilis*	ELSP	surface	4.3	0.2
Storm-petrel species	*Oceanodrama* spp.	STPE	surface	38.3	6.4
White-tailed Tropicbird	*Phaethon lepturus*	WTTR	plunge	2.1	0.3
Red-billed Tropicbird	*Phaethon aethereus*	RBTR	plunge	19.2	3.4
Masked Booby	*Sula dactylatra*	MABO	plunge	29.8	7.1
Red-footed Booby	*Sula sula*	RFBO	plunge	17.0	9.6
Brown Pelican	*Pelecanus occidentalis*	BRPE	plunge	2.1	0.1
Frigatebird species	*Fregata* spp.	FRIG	surface	8.5	0.5
Pomarine Jaeger	*Stercorarius pomarinus*	POJA	surface	2.1	0.1
Bonaparte's Gull	*Larus philadelphia*	BOGU	surface	2.1	0.1
Western Gull	*Larus occidentalis*	WEGU	surface	2.1	0.2
Glaucous-winged Gull	*Larus glaucescens*	GWGU	surface	2.1	1.5
Swallow-tailed Gull	*Creagrus furcatus*	STGU	surface	8.5	2.1
Common Tern	*Sterna hirundo*	COTE	plunge	4.3	0.5
Sooty Tern	*Sterna fuscata*	SOTE	plunge	2.1	0.8
Tern species	*Sterna* spp.	TERN	plunge	2.1	4.5
Noddy species	*Anous* spp.	NODD	plunge	4.3	0.3
Rhinoceros Auklet	*Cerorhinca monocerata*	RHAU	dive	2.1	0.1
Tufted Puffin	*Fratercula cirrhata*	TUPU	dive	6.4	0.6

different ecotones (onshore – offshore) and latitudinal regions (tropical – subarctic) (Fig. 2).

The first group, offshore-tropical, included Masked and Red-footed Boobies *Sula sula* and two associated species (Red-billed Tropicbird *Phaethon aethereus* and frigatebirds). The second group, offshore-subarctic, included the Black-footed Albatross, Northern Fulmar, Sooty Shearwater, and Leach's Storm-petrel. These two groups were linked by an associated species, the Red-billed Tropicbird. Additionally, each of these two offshore groups were linked with an onshore group with an affinity for tropical and subarctic waters. The third group, onshore-subarctic, included the Fork-tailed Storm Petrel *Oceanodroma furcata*, Wilson's Storm Petrel *Oceanites oceanicus* and Tufted Puffin *Fratercula cirrhata* and was linked with the offshore–subarctic group. The final group, onshore-tropical, included the Madeiran and Wedge-rumped Storm Petrel *Oceanodroma castro*, *O. tethys*, Pink-footed Shearwater *Puffinus creatopus* and Swallow-tailed Gull *Creagrus furcata* and was linked to the offshore-tropical taxa. We detected no associations between the species in the offshore-subarctic and onshore-tropical groups, or between the offshore-tropical and onshore-subarctic taxa (Fig. 2).

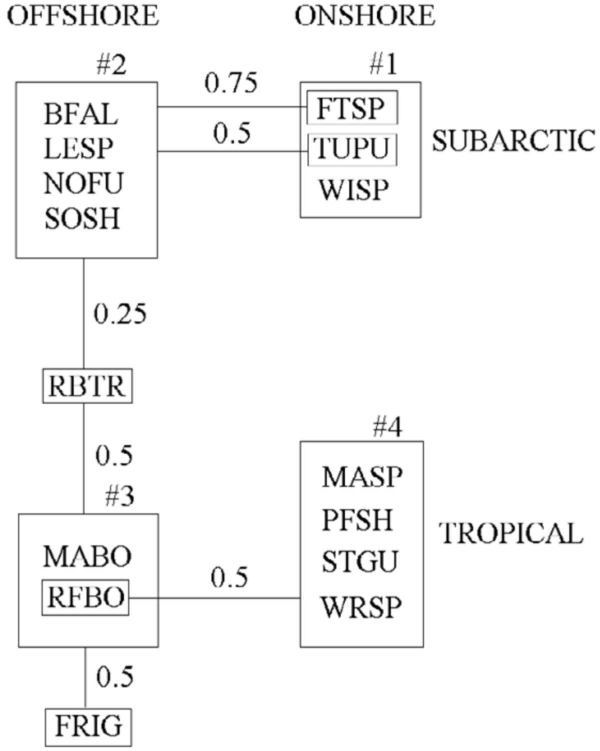

Fig. 2. Recurrent species groups formed using the daily observations of 15 "common" species sighted during the cruise. Individual species from one group may be linked to another group, if they have a positive affinity for some, but not all, of the taxa in the second recurrent group. These species – group linkages are labeled to show the magnitude (0-1) of these associations.

Oceanographic setting

The vessel was becalmed on 13 days from 0.35° N, 41.72° W to 38.43° N, 136.53° W, with extended no wind periods during 21-23 April and 18-21 May 1999. Average wind speeds at the 47 daily noon locations ranged from 1.58-9.64 m s^{-1} (Fig. 3A), with values 1-2 m s^{-1} lower than the long-term average along the tropics (10° S-15° N) and positive anomalies (1-2 m s^{-1} higher) off the West Coast of North America (30-40° N) (Fig. 3B).

The survey track traversed tropical, subtropical, and subarctic water masses, with surface temperatures at daily noon locations declining from 28.78 to 9.76º C moving northward (Fig. 4A). Ocean temperatures were largely cooler than the 50-year average for the NE Pacific, with the largest negative anomalies (1-2º C colder) north of 15º N latitude (Fig. 4B). We surveyed waters off the continental shelf, with ocean depth at the 47 daily locations ranging between 295 and 5,363 m. The daily SeaWiFS-derived median chlorophyll values ranged from 0.06 to 4.48 mg m^{-3} (Fig. 5).

Multivariate analysis of seabird assemblages

The NMDS procedure selected three habitat axes, which accounted for 88% of the variability observed in the structure of the marine bird community (Fig. 6). The first axis described onshore – offshore gradients associated with concurrent changes in ocean depth and chlorophyll concentration, with shallow shelf-slope regions supporting higher phytoplankton standing stocks. The second axis illustrated latitudinal/longitudinal changes in sea

TABLE 3
Summary of seabird orders and families recorded across the northeast Pacific, 20 April - 5 June 1999, showing the proportion of sighted birds that were identified to species level and the number of species identified.

Order	Family	Birds Sighted	Birds Identified	Proportion Identified	Species Identified
Procellariiformes	Diomedeidae	106	106	100.00	2
	Hydrobatidae	230	170	73.91	6
	Procellariidae	328	280	88.33	9
Pelecaniformes	Fregatidae	5	0	0.00	0
	Pelecanidae	1	1	100.00	1
	Phaethontidae	36	36	100.00	2
	Sulidae	162	162	100.00	2
Charadriiformes	Alcidae	7	7	100.00	2
	Laridae	38	38	100.00	4
	Stercorariidae	1	1	100.00	1
	Sternidae	60	13	21.67	2
TOTAL		**974**	**814**	**83.57**	**32**

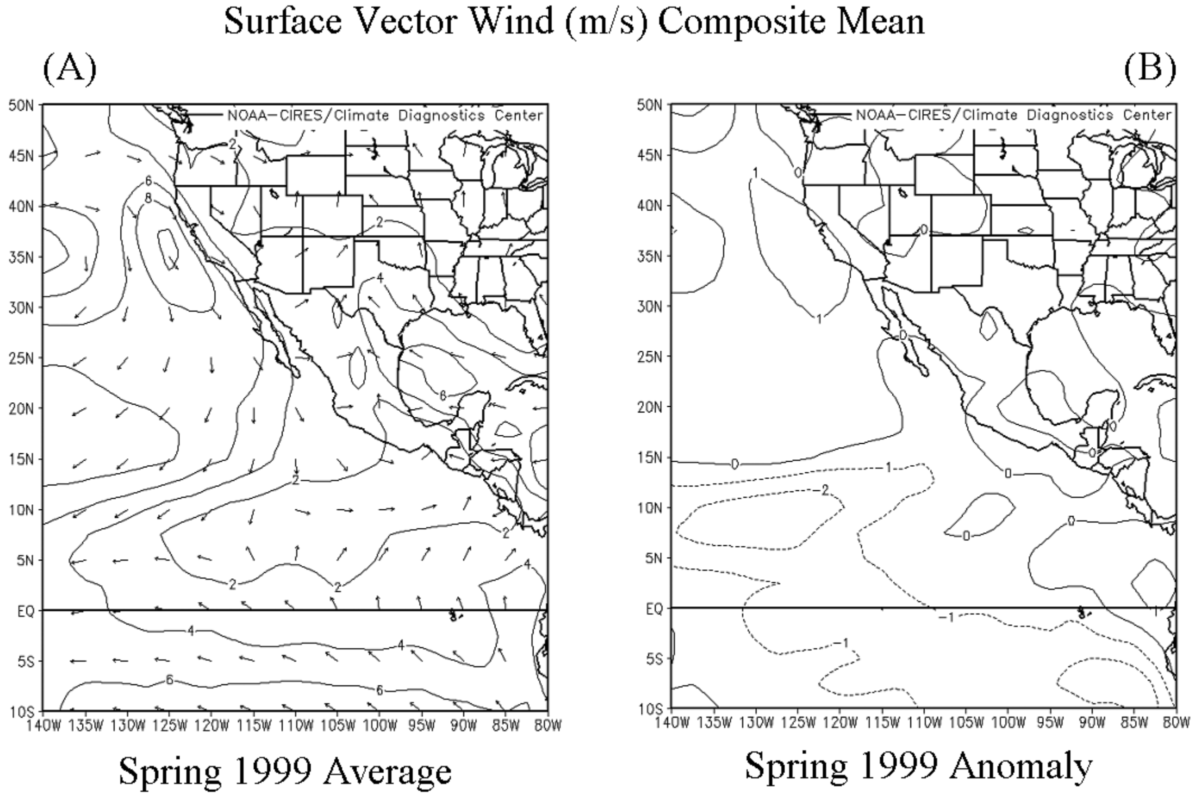

Fig. 3. Mean (A) and long-term anomaly (B) of wind speed during April-June 1999. The anomalies are calculated by subtracting the long-term seasonal climatology (1949-2003) from the mean values during 1999. Positive and negative values are indicative of anomalously higher and lower wind speeds during the 1999 cruise. Figure courtesy of NOAA's Climate Diagnostics Center (www.cdc.noaa.gov).

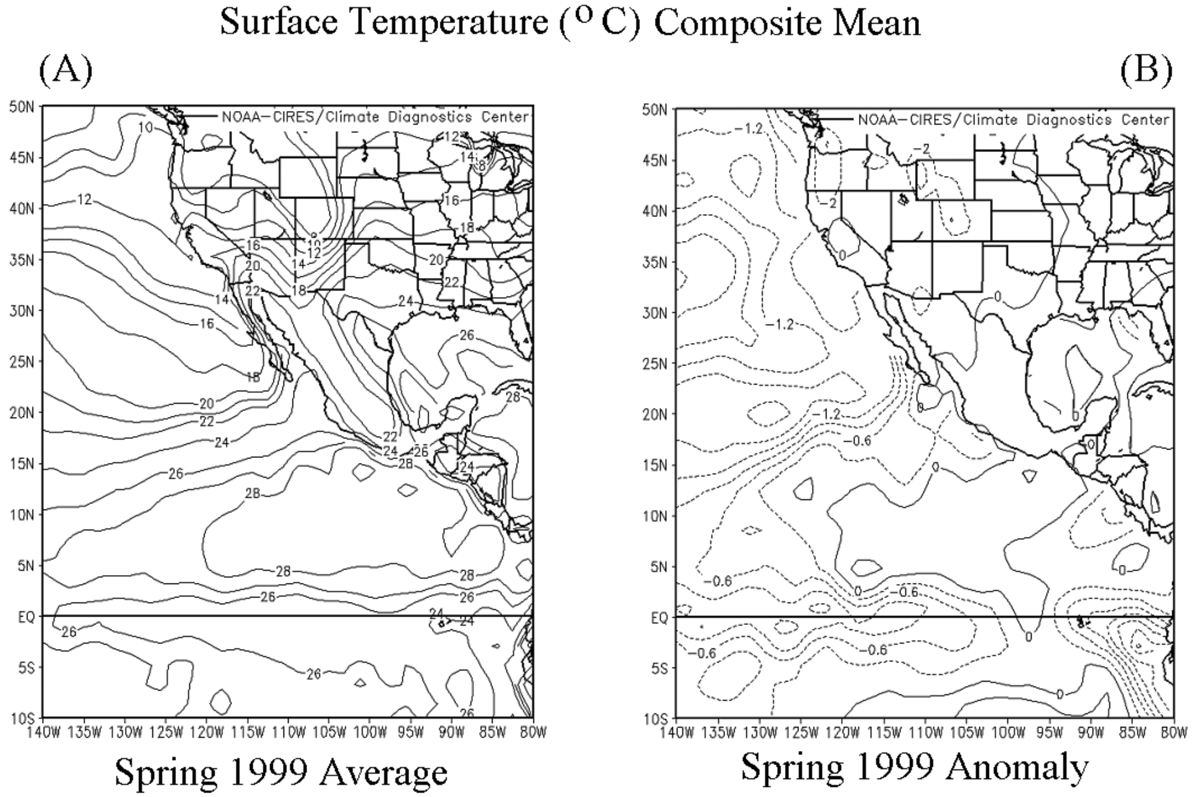

Fig. 4. Mean (A) and long-term anomaly (B) of sea surface temperature during April-June 1999. The anomalies are calculated by subtracting the long-term seasonal climatology (1949-2003) from the mean values during 1999. Positive and negative values are indicative of anomalously higher and lower wind speeds during the 1999 cruise. Figure courtesy of NOAA's Climate Diagnostics Center (www.cdc.noaa.gov).

surface temperature, with cooler ocean temperatures at more northern latitudes and western longitudes. The third axis included these same latitudinal/longitudinal ocean temperature gradients, as well as changes in mean ocean depth and wind speed (Table 4). Because sea surface temperature was strongly correlated with the second and third habitat axes selected by the NMDS procedure, we felt justified contrasting the composition of the avifauna within different water masses defined by specific SST ranges.

The NMDS plot reinforced the results of the recurrent group analysis. The seven species in the offshore-subarctic and the onshore-subarctic groups were associated with high wind speeds and cool water temperatures to the north and west of the area surveyed. A second cluster containing the seven tropical species occurred in warmer waters to the south and east of the study area. Furthermore, the Red-billed Tropicbird – a species associated with the two offshore recurrent groups – was plotted between the tropical and the subarctic NMDS species clusters (Figs. 2, 6).

Segregation across water masses

We found three seabird communities based on water mass characteristics: (1) a tropical community (booby – tropicbird – frigatebird) found exclusively in the warm subtropical frontal zone and tropical water mass (SST > 18° C); (2) a subarctic community (alcid – fulmar) largely restricted to subarctic and Transition Domain waters (SST: 9.7-17. 9° C); and (3) a widely-distributed, cosmopolitan community (storm-petrel – shearwater – albatross) occupying a broad range of ocean temperatures, from 9.7-28.8° C (Fig. 7).

In spite of the presence of diving birds in all water masses (due to the migratory movements of shearwaters), there was a significant segregation of seabird foraging guilds, as suggested by the number of pursuit diving, plunging, and surface foraging birds sighted in each of the five water masses we surveyed (G_8 = 246.02, P < 0.001). Plunge-divers were the numerically-dominant taxa in tropical waters, and divers were disproportionately more abundant in the cool waters of the Subarctic and Transition domains (Fig. 8). In addition to faunal disparities across water masses, we documented several frontal crossings along the survey track.

The SST gradients and the accumulation of marine debris and neustonic invertebrates suggest that we crossed two convergence zones associated with oceanic fronts: the Subtropical Frontal Zone

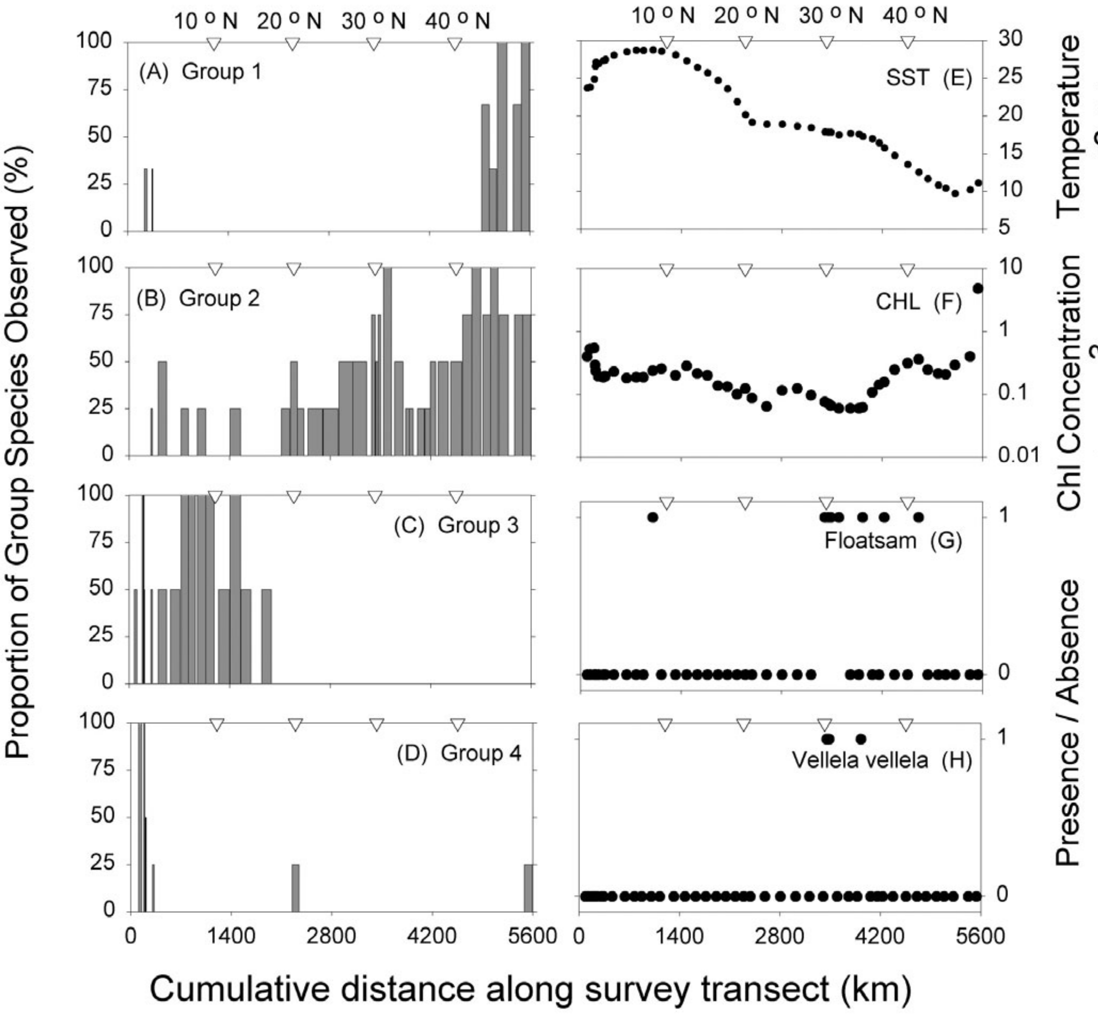

Fig. 5. Spatial distribution of recurrent group member species (A-D), water mass properties (E-F), floating debris (G) and neustonic zooplankton (H) along the 5,600 km track linking daily noon cruise positions (April 20-June 5, 1999). For each recurrent group, the proportion of the constituent species sighted on every survey day is plotted. Thus, the four recurrent group histograms for any given day need not add to 100%.

(SST: 18-20° C) at ~20° N, and the southern extent of the North Pacific Transition Zone (SST: 15-18° C) at ~35° N (Fig. 5E). Floating garbage (including discarded net, rope, styrofoam, plastic balls, buoys, and bottles) was observed beside the vessel on seven days, and was concentrated from 29° N; 133° W to 41° N; 137° W (Fig. 5G). Black-footed Albatross fed on small, floating plastic fragments, and fulmars and albatross found pelagic invertebrates that had accumulated on or near the flotsam. Large aggregations of Velella velella extended over 668 km (~ 30-35° N) in mid-May (Figure 5H).

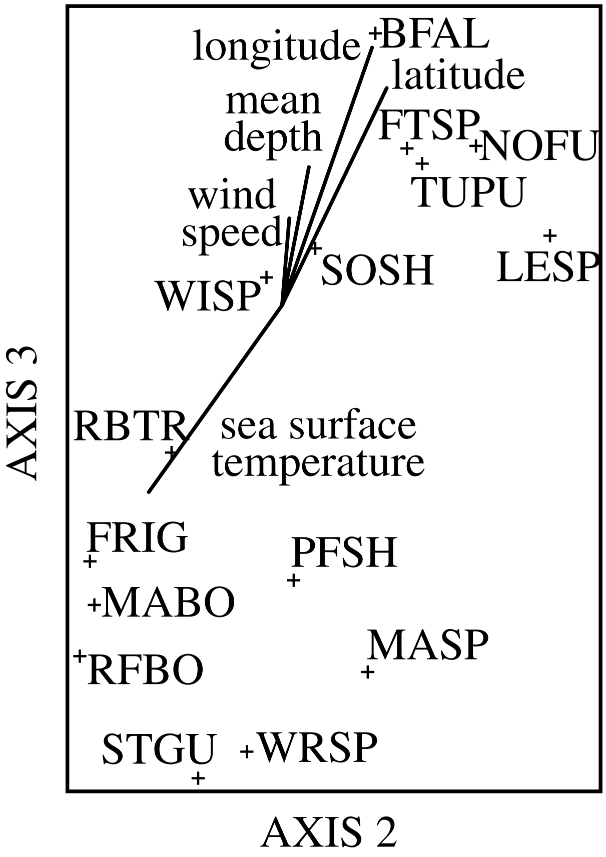

Fig. 6. Non-metric multidimensional scaling (NMDS) plot, showing the oceanographic habitats of the 15 "common" seabird species sighted during the cruise.

TABLE 4
Correlation coefficients between the six environmental variables and the three non-metric multidimensional scaling (NMDS) axes used to characterize marine bird oceanographic habitats.

Environmental Variable	Axis 1	Axis 2	Axis 3
Sea surface temperature (SST)	0.117	- 0.602	- 0.714
Wind speed (WSP)	0.155	0.207	0.482
Depth (DPH)	0.286	0.266	0.440
Latitude (LAT)	0.002	0.535	0.770
Longitude (LON)	0.187	0.496	0.834
Chlorophyll concentration (CHL)	- 0.206	- 0.025	- 0.009

DISCUSSION

This is the first study to examine seabird assemblages along a latitudinal gradient extending from tropical to subarctic waters in the eastern Pacific Ocean. Our analysis of the avifauna along a 9 000 km survey complement previous studies of marine bird communities in this region (Wahl *et al*. 1989, Gould & Piatt 1993) and similar studies in the tropical and south Pacific (Pitman 1986, Ribic & Ainley 1988, Ballance *et al*. 1997). This study revealed the spatial segregation of different species types and foraging guilds across water masses, defined in terms of sea surface temperature. These patterns were particularly striking for alcids that are restricted to cool subarctic waters (SST 12-9° C) and frigatebirds and boobies in tropical waters (SST > 20° C). Furthermore, while some species were restricted to specific water masses, other taxa occupied a broad range of ocean temperatures. In particular, the Black-footed Albatrosses, Northern Fulmars, and Red-billed Tropicbirds inhabited several "adjacent" water masses characterized by similar properties. The fulmars were found in subarctic, Transition Domain, and subtropical waters, while the tropicbirds occupied warmer tropical and subtropical front waters. As suggested by both the recurrent group analysis and the multidimensional scaling plot, the Red-billed Tropicbird inhabits a "transitional" habitat between the tropical species to the south and the subarctic taxa to the north. The broad distribution of the Black-footed Albatross suggests that this species occupies a wide range of ocean temperatures but aggregates at the North Pacific Transition Domain and the subtropical frontal zone (Wahl *et al*. 1989, Hyrenbach *et al*. 2002). Finally, other cosmopolitan species groups, like storm petrels and shearwaters, were found in all water masses. This result is not unexpected, as these are very specious groups, including warm-water and cold-

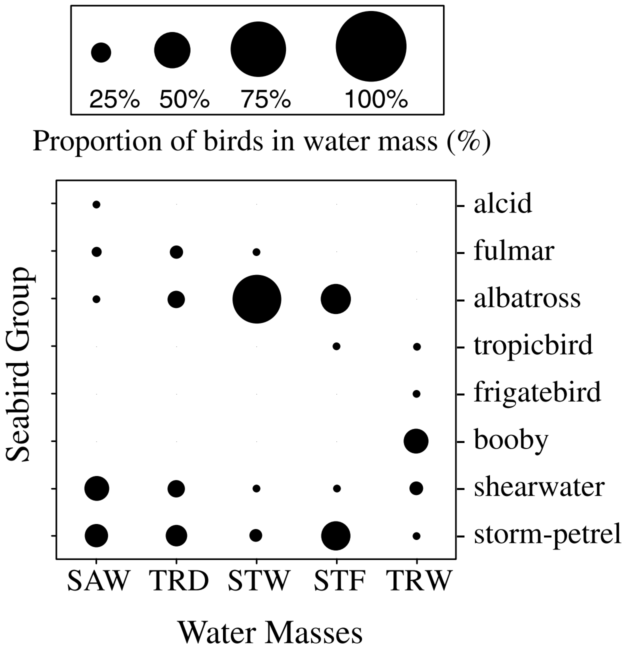

Fig. 7. Make-up of the seabird communities inhabiting different North Pacific water masses, defined in terms of sea surface temperature characteristics. The circles are proportional to the relative abundance of different seabird species groups. The totals for each water mass need not add to 100% if other taxa were sighted.

water taxa with tropical and subpolar distributions (Harrison 1985). In particular, our survey overlapped with the spring, northward migration of the southern hemisphere shearwaters and we found these birds scattered throughout the study area (Gould & Piatt 1993, Spear & Ainley 1999).

Significance of distinct water masses

The segregation of species types and foraging guilds across water masses underscores the notion that seabirds with different life-styles preferentially occupy specific oceanic domains (Ainley 1977, Wahl *et al*. 1989, Ballance *et al*. 1997, Spear & Ainley 1998). Previously, Wahl and coworkers (1989) documented similar segregation patterns of pursuit diving and plunge diving species across the North Pacific during summer, with pursuit divers preferentially inhabiting cool and highly-productive subarctic waters and plunge divers being most numerous in the warmer and less productive waters of the Subtropical Gyre. Similar patterns have been observed for breeding seabird communities along the eastern North Pacific, from the Galápagos (0º N) to Olympic Island (48º N) (Ainley 1977). Ultimately, the dispersion of prey resources and the energetic constraints of foraging influence whether seabird species can inhabit specific water masses.

In this study, we found that three habitat axes accounted for a large proportion (88%) of the structure of the marine avifauna. Additional environmental variables not addressed in this study (e.g. the distribution of prey resources and the distance to breeding colonies) probably account for the unexplained variance. Sea surface temperature proved to be a very strong determinant of seabird community structure, as previously documented by other studies in the Pacific Ocean (e.g., Ribic & Ainley 1988, Wahl *et al.* 1989, Hyrenbach & Veit 2003). Because the habitat axes were strongly correlated with water temperature, we investigated the distribution of different species and foraging guilds across specific water masses. These water mass associations seemed particularly relevant given the fluid nature of oceanic systems, and the well-established temperature associations of many of the prey exploited by marine birds. Moreover, because the location of frontal systems and the extent of water masses shift seasonally and from year to year, the study of temperature associations facilitates comparisons across time and space (McKinnell & Waddell 1993, Lehodey *et al*. 1997, Hyrenbach & Veit 2003).

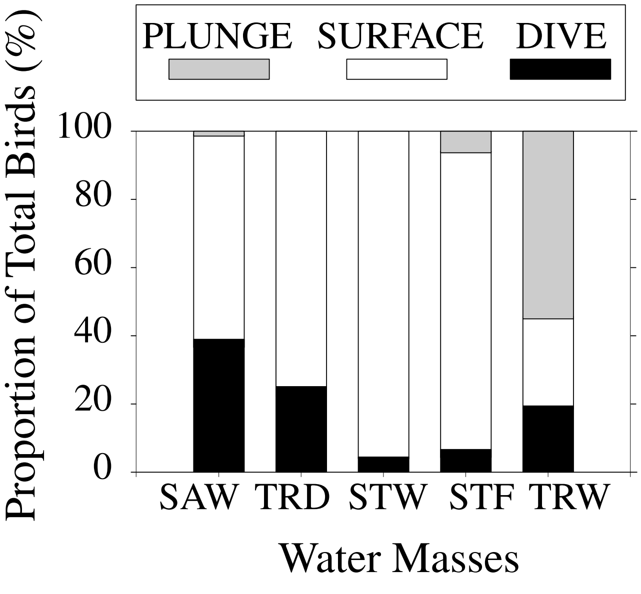

Fig. 8. Proportion of different seabird foraging guilds inhabiting different North Pacific water masses, defined in terms of sea surface temperature characteristics.

Significance of frontal systems

The sea surface temperature (SST) gradients, and the presence of floating debris and *Velella velella* along the track suggest our survey crossed two frontal systems: one at ~20º N and another one at ~35° N. We observed a very striking latitudinal shift in seabird community structure over a relatively short distance (~200 km) in the vicinity of 20° N, which was associated with the Subtropical Frontal Zone (SST: 20-18° C). This observation underscores the significance of oceanic fronts and water mass boundaries as important biogeographic features in the open ocean (Sverdrup *et al*. 1942, Fager & McGowan 1963, Longhurst 1998). In pelagic systems, changes in the types and abundances of nektonic organisms (marine mammals, seabirds, large predatory fishes) often occur at frontal systems, where waters of different temperature and salinity meet (Gould & Piatt, 1993, Brodeur *et al*., 1999). Previously, researchers documented changes in seabird communities across similar hydrographic fronts in the eastern North Pacific. A narrow (40-44º N) region of strong temperature and salinity gradients, termed the Transition Domain, delimits the ranges of subarctic and subtropical species, and influences the distribution of far-ranging fish, seabirds, and marine mammals (McKinnell & Waddell 1993, Brodeur *et al.* 1999, Springer *et al.* 1999).

Frontal systems and convergence zones concentrate marine debris and neustonic prey across the North Pacific Ocean (Dahlberg & Day 1985, Galt 1985). Procellarids may ingest small pieces of plastic while foraging in these areas (Blight & Burger 1997), leading to a decline in body condition (Sileo *et al*. 1990).

Significance of prevailing wind patterns

In addition to water mass distributions and frontal systems, prevailing wind patterns are potentially important determinants of seabird distributions and community structure (Spear & Ainley 1998, Weimerskirch *et al*. 2000). In the northeast Pacific, there is a marked reduction in surface winds from 25-35° N associated with a subtropical anticyclone, a zone typically referred to as the 'horse latitudes' by offshore sailors. As expected, there were very light winds from 15-30° N during the spring of 1999. However, winds were also exceptionally light south of 15° N, an area known for favourable tradewinds. The collapse of the climatological wind patterns, with relatively light winds across the entire track, might explain the relatively low number of total birds seen during this cruise.

Large-scale oceanographic context

Ocean conditions are dynamic and change from year to year, thus it is essential that we place our observations in a larger, oceanographic context. During the fall of 1998, a strong La Niña event developed in the northeast Pacific. By August 1998, the multivariate ENSO index changed from a positive value, indicative of El Niño conditions, into a negative value, suggestive of a developing La Niña event. By September, the eastern tropical Pacific (5º N-5º S; 90-150º W) was characterized by anomalously shallow thermocline depths (Bograd *et al.* 2000); and strong negative SST anomalies (exceeding 1° C) were apparent along the tropics and off the West Coast of North America (Hayward *et al.* 1999). Unusually high coastal upwelling off the West Coast of

North America (21-51° N) persisted from the fall of 1998 to the fall of 1999, resulting in the unusually cold SSTs observed during this cruise (Bograd *et al*. 2000, Schwing *et al*. 2000). However, it is unclear to what extent these atmospheric and oceanographic perturbations influenced the avifauna of the northeast Pacific Ocean. Additional cruises will be required to determine whether the anomalous conditions during the spring of 1999 lead to unusual seabird distributions and marine bird community structure.

Our study suggested that, over macro-mega spatial scales (1000s km), marine bird communities of the northeast Pacific Ocean are associated with distinct water masses. Moreover, the observed segregation of different foraging guilds suggests that marine bird communities are structured by the interplay of ocean productivity and the costs of foraging. This cruise followed an unusual track during an anomalous year. Thus, additional surveys are required to assess how the marine bird communities of the northeast Pacific Ocean shift spatially and temporally.

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REFERENCES

AINLEY, D.G. 1977. Feeding methods of seabirds: a comparison of polar and tropical nesting communities in the eastern Pacific Ocean. In: Llano, G.A. (Ed). Adaptations within Antarctic ecosystems. Houston, Gulf Publishing Company. pp. 669-686.

ASHMOLE, N.P. 1971. Sea bird ecology and the marine environment. In: Farner, D.S. & King, J.R. (Eds.), Avian Biology. Vol. 1. New York, Academic Press. pp. 669-686.

BALLANCE, L.T., PITMAN, R.L. & REILLY, S.B. 1997. Seabird community structure along a productivity gradient: importance of competition and energetic constraint. *Ecology* 78: 1502-1518.

BARBER, R.T. & CHAVEZ, F.P. 1986. Ocean variability in relation to living resources during the 1982-83 El Niño. *Nature* 319: 279-285.

BLIGHT, L. & BURGER, A. 1997. Occurrence of plastic particles in seabirds from the Eastern North Pacific. *Marine Pollution Bulletin* 34(5): 323-325.

BOGRAD, S.J., DIGIACOMO, P.M., DURAZO, R., HAYWARD, T.L., HYRENBACH, K.D., LYNN, R.J., MANTYLA, A.W., SCHWING, F.B., SYDEMAN, W.J., BAUMGARTNER, T., LAVANIEGOS, B. & MOORE, C.S. 2000. The state of the California Current, 1999-2000: forward to a new regime ? *CalCOFI Reports* 41: 26-52.

BRODEUR, R., MCKINNELL, S., NAGASAWA, K., PEARCY, K., RADCHENKO, V. & TAGAKI, S. 1999. Epipelagic nekton of the North Pacific subarctic and Transition Zones. *Progress in Oceanography* 43: 365-397.

CHAVEZ, F.P., COLLINS, C.A., HUYER, A. & MACKAS, D.L. 2002. El Niño along the west coast of North America. *Progress in Oceanography* 54: 1-5 2002.

CHAVEZ, F.P., RYAN, J., LLUCH-COTA, S.E. & ÑIQUEN, M.C. 2003. From Anchovies to sardines and back: multidecadal change in the Pacific Ocean. *Science* 299: 217-221.

CLANCY, R.M. 1992. Operational modeling: ocean modeling at the Fleet Numerical Oceanography Center. *Oceanography* 5: 31-35.

CORNELL, J. 1992. World Cruising Routes. London, McGraw-Hill International Marine Publishing Company, London. 480 p.

DAHLBERG, M.L. & DAY, R.H. 1985. Observations of man-made objects on the surface of the North Pacific. In: Shomura, R.S. & Yoshida, H. O. (Eds.), Proceedings of the workshop on the fate and impact of marine debris, 27-29 November 1984, Honolulu, U. S. Department of Commerce, NOAA Technical Memorandum, NMFS, NOAA-TM-NMFS-SWFC-54. pp. 198-212.

FAGER, E.W. 1957. Determination and analysis of recurrent groups. *Ecology* 38: 586-595.

FAGER, E.W. & MCGOWAN, J.A. 1963. Zooplankton species groups in the North Pacific. *Science* 140: 453-461.

GALT, J.A. 1985. Oceanographic factors affecting the predictability of drifting objects at sea. In: Shomura, R.S. & Yoshida, H. O. (Eds.), Proceedings of the workshop on the fate and impact of marine debris, 27-29 November 1984, Honolulu, U.S. Department of Commerce, NOAA Technical Memorandum, NMFS, NOAA-TM-NMFS-SWFC-54. pp. 497-507.

GARTHE, S. & HüPPOP, O. 1999. Effect of ship speed on seabird counts in areas supporting commercial fisheries. *Journal of Field Ornithology* 70: 28-32.

GOULD, P.J. & PIATT, J.F. 1993. Seabirds of the central North Pacific. In: K. Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds.), The status, ecology, and conservation of marine birds of the North Pacific. Ottawa, Canadian Wildlife Service Special Publication. pp. 27-38.

HARRISON, P. 1985. Seabirds. An Identification Guide. Boston: Houghton Mifflin Co.

HAYWARD, T.L., BAUMGARTNER, T.R., CHECKLEY, D.M., DURAZO, R., GAXIOLA-CASTRO, G., HYRENBACH, K.D., MANTYLA, A.W., MULLIN, M.M., MURPHREE, T., SCHWING, F.B., SMITH, P.E. & TEGNER, M.J. 1999. The state of the California Current, 1998-1999: transition to cool-water conditions. *CalCOFI Reports* 40: 29-62.

HOOKER, S.B. & MCCLAIN, C.R. 2000. The calibration and validation of SeaWiFS data. *Progress in Oceanography* 45 (3-4): 427-465.

HYRENBACH, K.D., FERNANDEZ, P. & ANDERSON, D.J. 2002. Oceanographic habitats of two sympatric North Pacific albatrosses during the breeding season. *Marine Ecology Progress Series* 233: 283-301.

HYRENBACH, K.D. & VEIT R.R. 2003. Ocean warming and seabird communities of the California Current System: response at multiple temporal scales. *Deep-Sea Research II* 50 (14-16): 2537-2565.

KAHRU, M. & MITCHELL, B.G. 1999. Empirical chlorophyll algorithm and preliminary SeaWiFS validation for the California Current. *International Journal of Remote Sensing* 20: 3423-3429.

KENKEL N.C. & ORLOCI, L. 1986. Applying metric and nonmetric multidimensional scaling to ecological studies: some new results. *Ecology* 67: 919-923.

LEHODEY P., BERTINAC M., HAMPTON J., LEWIS A. & PICAUT J. 1997. El Niño southern Oscillation and tuna in the western Pacific. *Nature* 389: 715-718.

LONGHURST, A. 1998. Ecological geography of the sea. San Diego, Academic Press.

LYNN, R.J. 1986. The subarctic and northern subtropical fronts in the eastern North Pacific Ocean in spring. *Journal of Physical Oceanography* 16: 209-222.

MANTUA, N.J., HARE, S.R. ZHANG, Y., WALLACE, J.M. & FRANCIS, R.C. 1997. A Pacific interdecadal climate oscillation with impacts on salmon production. *Bulletin of the American Meteorological Society* 78: 1069-1079.

MCCLAIN, E.P., PICHEL, W.G. & WALTON, C.C. 1985. Comparative performance of AVHRR-based multichannel sea surface temperatures. *Journal of Geophysical Research* 90: 11587-11601.

MCCUNE, B. & MEFFORD, M.J. 1999. PC-ORD: Multivariate analysis of ecological data (version 4). Gleneden Beach, MjM Software Design.

MCKINNELL, S. & WADDELL, B. 1993. Associations of species caught in the Japanese large scale pelagic squid driftnet fishery in the Central North Pacific Ocean: 1988-1990. *International North Pacific Fisheries Commission Bulletin* 53: 91-146.

NGDC (National Geophysical Data Center). 1998. Data Announcement 88-MGG-02, Digital relief of the surface of the Earth. Boulder: National Geophysical Data Center. (www.ngdc.noaa.gov/mgg/global/seltopo.html).

PITMAN, R.L. 1986. Atlas of seabird distribution and relative abundance in the eastern tropical Pacific. Administrative Report LJ-86-02C. Southwest Fisheries Center, La Jolla, CA.

POLOVINA, J.J. 1996. Decadal variation in the trans Pacific migration of northern Bluefin Tuna (*Thunnus thynnus*) coherent with climate induced change in prey abundance. *Fisheries Oceanography* 5 (2): 114-119.

POLOVINA, J.J., MITCHUM, G.T., GRAHAM, N.E., MITCHELL, P.C., DEMARTINI, E.E. & FLINT, E.B. 1994. Physical and biological consequences of a climate event in the Central North Pacific. *Fisheries Oceanography* 3:15-21.

REYNOLDS, R.W. & SMITH, T.M. 1994. Improved global sea surface temperature analyses using optimum interpolation. *Journal of Climate* 7: 929-948.

RIBIC, C.A. and D.G. AINLEY. 1988. Constancy of seabird assemblages; an exploratory look. *Biological Oceanography* 6: 175-202.

RODEN, G.I. 1991. Subarctic-subtropical transition zone of the North Pacific: large scale aspects and mesoscale structure. In: Wetherall, J.A. (Ed.), Biology, oceanography, and fisheries of the North Pacific Transition Zone and Subarctic Frontal Zone: Papers from the North Pacific Transition zone workshop, 9-11 May 1988. NOAA Technical Report NMFS 105. Honolulu, U.S. Department of Commerce. pp. 1-38.

SCHNEIDER, D.C., HUNT, G.L., Jr. & HARRISON, N.M. 1986. Mass and energy transfer to pelagic birds in the southeastern Bering Sea. *Continental Shelf Research* 5: 241-257.

SCHWING, F.B., MOORE, C.S., RALSTON, S. & SAKUMA, K.M. 2000. Record coastal upwelling in the California Current during 1999. *CalCOFI Reports* 41: 148-160.

SHIMOTO, A., ISHIDA, Y., TAMAKI, M. & YAMANAKA, Y. 1998. Primary production and chlorophyll a in the northwestern Pacific Ocean in summer. *Journal of Geophysical Research* 103: 24651-24661.

SILEO L., SIEVERT P.R. & SAMUEL, M.D. 1990. Causes of mortality of albatross chicks at midway atoll. *Journal of Wildlife Diseases* 26: 329-338.

SPEAR, L.B. & AINLEY, D.G. 1998. Morphological differences relative to ecological segregation in petrels (Family: Procellariidae) of the Southern Ocean and tropical Pacific. *Auk* 115: 1017-1033.

SPEAR, L.B. & AINLEY, D.G. 1999. Migration routes of Sooty Shearwaters in the Pacific Ocean. *Condor* 101: 205-218.

SPEAR, L.B., NUR, N. & AINLEY, D.G. 1992. Estimating absolute densities of flying seabirds using analyses of relative movement. *Auk* 109: 385-389.

SPRINGER, A.M., PIATT, J. F., SHUNTOV, V. P. & VAN VLIET, G.B. 1999. Marine birds and mammals of the Pacific Subarctic Gyres. *Progress in Oceanography* 43: 443-487.

STAHL, J.C., JOUVENTIN, P., MOUGIN, J. L., ROUX, J.P., & WEIMERSKIRCH, H. 1985. The foraging zones of seabirds in the Crozet Islands sector of the Southern Ocean. In: Siegfried, W.R., Condy, P.R. & Laws, R.M. (Eds.), Antarctic Nutrient Cycles and Food Webs. Proceedings of the 4th Symposium on Antarctic Biology. Berlin, Springer-Verlag. pp. 478-486.

SVERDRUP, H.U., JOHNSON, M.J. & FLEMING, R.H. 1942. The Oceans. Their Physics, Chemistry and General Biology. Englewood Cliffs, Prentice Hall.

TASKER, M.L., HOPE-JONES, P., DIXON, T. & BLAKE, B.F. 1984. Counting seabirds at sea from ships: a review of methods employed and suggestion for a standardized approach. *Auk* 101: 567-577.

VEIT, R.R. 1995. Pelagic communities of seabirds in the South Atlantic Ocean. *Ibis* 137: 1-10.

VENRICK, E.L. 1982. Phytoplankton in an oligotrophic ocean: observations and questions. *Ecological Monographs* 52: 129-154.

VENRICK, E.L., MCGOWAN, J.A., CAYAN, D.R. & HAYWARD, T.L. 1987. Climate and chlorophyll a: long-term trends in the Central North Pacific. *Science* 238: 70-72.

VINOGRADOV, M.E., SHUSKINA, E.A., VEDERNIKOV, V.I., NEZLIN, N.P. & GAGARIN, V.I. 1997. Primary production and plankton stocks in the Pacific Ocean and their seasonal variation according to remote sensing and field observations. *Deep-Sea Research II* 44: 1979-2001.

WAHL, T.R., AINLEY, D.G., BENEDICT, A.H. & DEGANGE, A.R. 1989. Associations between seabirds and water masses in the northern Pacific Ocean in summer. *Marine Biology* 103: 1-11.

WEIMERSKIRCH, H., GUIONNET, T., MARTIN, J., SHAFFER, S.A., COSTA, D.P. & WILSON, R.P. 2000. Fast and fuel efficient? Optimal use of wind by flying albatrosses. *Proceedings of the Royal Society of London B* 267: 1869-1874.

ZAR, J.H. 1984. Biostatistical Analysis. New Jersey, Prentice-Hall.

COMPARISON OF COLONIAL BREEDING SEABIRDS IN THE EASTERN BERING SEA AND GULF OF ALASKA

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SUMMARY

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We examined populations of colonial breeding seabirds in Alaska. We compared data on populations from the eastern Bering Sea (EBS) and the Gulf of Alaska (GOA) using U.S. Fish and Wildlife Service (USFWS) data from the Beringian Seabird Colony Database. The EBS and GOA are vast areas that support large diverse populations of breeding seabirds. Seabird distribution in Alaska is highly clumped: 12 of the 1714 colonies support 50% of all breeding birds, with most of these large colonies located in the EBS. The EBS has nearly three times as many seabirds as the GOA. The large numbers of seabirds in the EBS are due in part because the EBS is larger than the GOA and to the millions of planktivorous auklets that breed in the EBS but are virtually absent from the GOA. In the Bering Sea, Least *Aethia pusilla* and Crested *Aethia cristatella* Auklet colonies appear to be restricted to volcanic islands near highly productive upwelling areas in the central and western Aleutian Islands, the shelf-break in the central Bering Sea and the Anadyr Stream in the northern Bering Sea. They are conspicuously absent from the volcanic eastern Aleutian Islands east of Samalga Pass that are surrounded by warmer, fresher, water from the Alaska Coastal Current compared to the cooler, saltier oceanic water in the western and central Aleutians. The piscivorous species are more evenly distributed between the two regions. The most abundant piscivore, the Common Murre *Uria aalge*, is evenly split between the two regions. The EBS is more productive than the GOA, but both areas support similar biomass/km^2 of breeding seabirds. This pattern may in part be due to greater predation by foxes in the Bering Sea. Foxes still remain on some Aleutian Islands from introductions years ago and are indigenous on the northern Bering Sea Islands and the eastern Aleutian Islands. Relatively few islands in the GOA support foxes.

Keywords: distribution, oceanography, Bering Sea, auklets, *Aethia*, murres, *Uria* , piscivores, planktivores

INTRODUCTION

Present day seabird distributions are a product of many factors including: evolution, dispersal, predator-free nesting habitat, food resources, competition, and human influences (Ashmole 1963, Lack 1966, Udvardy 1974, Birkhead & Furness 1985). Seabirds generally live on predator-free islands with abundant food resources nearby. Their populations are often thought to be limited by food (Ashmole 1963, Lack 1966, Furness & Monaghan 1987, Springer 1991, Hunt *et al*. 1993). In Alaska, seabirds have been greatly affected by introduced predators (Bailey 1993), fisheries interactions (Degange *et al*. 1993), oils spills (Piatt *et al*. 1990), and climate change (Agler *et al*. 1999, Anderson & Piatt 1999). Nevertheless, Alaska still has some of the largest and most diverse seabird colonies in the North Hemisphere (Lensink 1984).

Alaska's breeding seabird population is estimated to be about 29 million birds composed of 35 species (USFWS 2004). Ninety-five percent of the colonial nesting seabirds in Alaska inhabit the large, diverse marine environments of the eastern Bering Sea (EBS) and Gulf of Alaska (GOA) (USFWS 2004). The seabird communities in the EBS and the GOA, however, are quite different from each other, being dominated by different species of birds (USFWS 2004). The objective of this study was to describe and compare some of the patterns of the seabird communities breeding in the rich areas of the EBS and the GOA, and to explore some of the potential factors that may contribute to differences in species composition and overall bird numbers between the two regions.

STUDY AREA

The study area is located in Alaska and is divided into 2 regions: the eastern Bering Sea (EBS) and the Gulf of Alaska (GOA) (Fig. 1). The EBS consists of coastal lands, islands, and waters between Alaska and Russia, including the Aleutian Islands, west side of the Alaska Peninsula, and the western Alaska coastline to the Seward Peninsula in the Bering Strait. The GOA includes southeast Alaska,

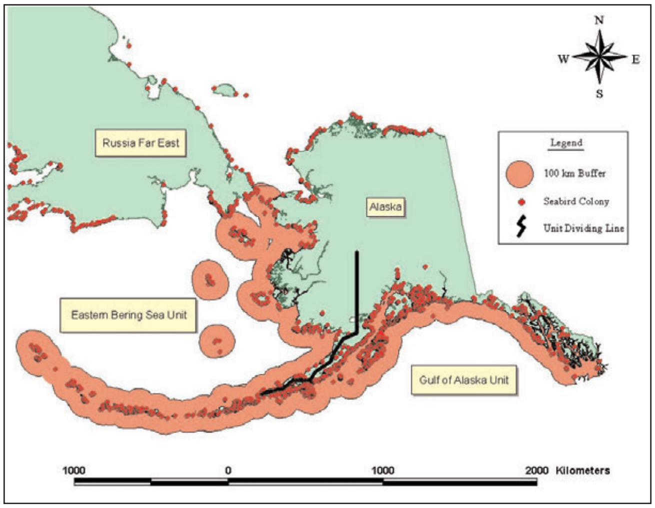

Fig. 1. Alaska seabird colony map with the eastern Bering Sea Unit and Gulf of Alaska Unit study areas identified (USFWS 2004).

Prince William Sound, Cook Inlet, Kodiak Archipelago, the east side of the Alaska Peninsula, and associated islands and waters.

METHODS

We examined populations of colonial breeding seabirds in the EBS and GOA. We then related the seabird parameters to colony site attributes and indices of ocean productivity. We used data from the Beringian Seabird Colony Database (Stephensen 2001, USFWS 2004), a computerized and expanded version of the Catalog of Alaskan Seabird Colonies (Sowls *et al*. 1978). The database stores current and historical data on breeding population sizes, species composition, and location of seabird colonies in Alaska and the Russian Far East. Population data in the database were obtained by counting or estimating breeding bird numbers using standardized techniques (USFWS 1999). These data have been collected over many years, by different observers, and using differing survey methods; thus inhibiting long-term comparisons due to the variable data quality (Stephensen & Mendenhall 1998). For this paper, we used the most representative estimates for each colony in the database (USFWS 1994). In most cases the most representative estimate is the most recent. However, sometimes an earlier census was deemed more reliable (e.g., if the colony was recently subject to disturbance or the recent census was conducted under poor conditions). We believe that the general patterns reported here are accurate, but remind readers that the actual numbers of breeding birds should be interpreted with caution. We used the following parameters in our analysis: number of colonies, colony size, seabird biomass, and foraging guilds. We calculated seabird biomass using published mean body mass data (Hunt *et al*. 2000) multiplied by species-specific population sizes (USFWS 2004). We excluded six species with populations below 100 individuals in our study area.

Thirty-one seabird species were grouped into 2 foraging guilds, piscivores and planktivores, using the dietary data compiled in Gaston and Hipfner (2000), Hatch (2002), and Hunt *et al*. (2000). Birds that eat squid were combined with the piscivores, and omnivores (species with broad diets) were placed into whichever prey category (fish-squid or plankton) was the dominant diet constituent. We calculated the total population and biomass for each guild in each area separately. Unidentified murres were classified as Common Murres *Uria aalge* or Thick-billed Murres *U. lomvia* based on the proportions of identified birds in each region.

To assess the degree of clumping of seabirds we ranked colonies by size and calculated how many colonies were needed to support half of a bird's total population. These colonies were deemed especially important for the species. We did this for all colonies, including mixed-species colonies, and for each species separately. Finally, we assessed the importance of each colony by adding up the number of species, for which that colony was deemed important (i.e., one of the colonies that were needed to support half of the breeding population).

We obtained data from the Alaska Volcano Observatory, U.S. Geological Survey (USGS) and compared land mass age and surface substrate (Beikman 1994, Miller *et al*. 1998) of nesting areas.

To compare the relative area available for foraging in the EBS and the GOA, we used a 100 km buffer around all colonies as an index of foraging range. If foraging area of two colonies overlapped, the overlap area was only counted once. Although many seabirds forage closer to the colony and many forage at greater distances, by using a single radius, we were able to compare the relative foraging area for the two regions. The seabird foraging habitat (100 km buffer) areas were calculated by selecting poly-lines of a geographic layer in ArcView GIS version 3.2 and performing a summary statistic function.

To investigate relative oceanic productivity of each area, we compared estimates of carbon produced per year (Springer *et al*. 1989, Springer & McRoy 1993), chlorophyll concentrations and summer plankton biomass (Sugimoto & Tadokoro 1997). Lacking data on forage fish, we also reviewed the 2003 fish stock abundance assessment and the 2002 groundfish catch data from the National Marine Fisheries Service (NMFS weekly production and observer reports).

RESULTS

About 29 million seabirds nest in 1 714 mixed species colonies in Alaska. The distribution of seabirds among these colonies is highly skewed. A few colonies have over a million birds while hundreds of colonies have fewer than 1 000 birds (USFWS 2004). Fifty percent of Alaska's seabirds breed in 12 massive, mixed-species colonies, the remainder are spread throughout other 1 702 colonies. Ten of the 12 largest colonies are in the EBS and two are in the GOA (Fig. 2).

Fifty percent of the populations of all Alaskan breeding species can be found within 148 colony sites. These colonies are split more evenly between the GOA and the EBS than the 12 largest colonies (Fig. 2). Forty of these 148 sites are important (i.e., one of the colonies needed to support 50% of a species breeding population) colonies for more than one species (Fig. 3).

The EBS supports almost three times as many seabirds as the GOA. The total breeding population of all seabird species in the EBS is approximately 20.3 million birds while the GOA has only 7.2 million (Table 1). Planktivorous seabirds are nearly five times as

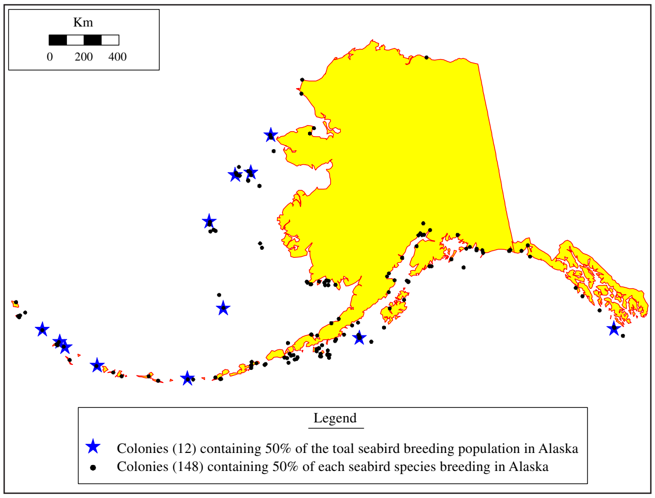

Fig. 2. Locations of the twelve seabird colonies containing half of the total breeding seabird population in Alaska and locations of 148 seabird colonies containing half of each seabird species breeding in Alaska (USFWS 2004).

abundant in the EBS as in the GOA, but piscivorous seabirds are only 1.6 times more numerous in the EBS (Table 1). Four planktivores, Crested Auklet *Aethia cristatella*, Least Auklet *Aethia pusilla*, Fork-tailed Storm-Petrel *Oceanodroma furcata*, and Leach's Storm-Petrel *Oceanodroma leucorhoa* and 1 piscivore; Thick-billed Murre account for 98% of the higher populations in the EBS (Fig. 4 & Appendix 2 & 3).

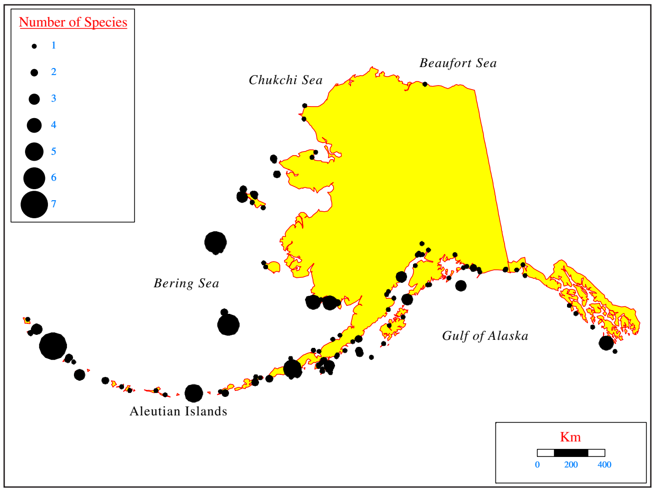

Fig. 3. Locations of 148 seabird colonies containing half of each seabird species breeding in Alaska, size of dot indicates how many species breed at each site (USFWS 2004).

TABLE 1

Comparison of seabird and groundfish parameters of the eastern Bering Sea and Gulf of Alaska (Hunt *et al*. 2000, NMFS 2002a, NMFS 2002b, NMFS 2003a, NMFS 2003b, Sugimoto and Tadokoro 1997, USFWS 2004). Add

Parameter	**Eastern Bering Sea**	**Gulf of Alaska**
Total foraging area (km^2)	942,552	549,763*
Total number of seabirds	20,870,286	7,156,926
Number of piscivorous seabirds	7,123,044	4,625,126
Number of planktivorous seabirds	13,747,242	2,531,800
Total seabird biomass (metric tons)	7,343	3,678
Piscivorous seabird biomass (metric tons)	5,773	3,461
Planktivorous seabird biomass (metric tons)	1,571	217
Total number of colonies	472	1,120
Median colony size	463	103
Number of seabird species	25	22
Chlorophyll concentration (mg m^{-3})**	1.88	1.35
Zooplankton biomass (mg m^{-3})**	386	221
2002 groundfish catch (metric tons)	1,760,275***	165,568***
2003 fish stock abundance (metric tons)	19,781,300***	4,005,170***

* Western Gulf of Alaska and SE Alaska foraging area 406,592 and 143,171 respectively.

** calculated mean from 1980-1994 from Sugimoto and Tadokoro 1997.

*** National Marine Fisheries Service (NMFS weekly production and observer reports).

Total seabird biomass in the EBS was 1.85 times higher than in the GOA (Table 1). This ratio is smaller than the ratio of numbers (2.82) because GOA supports a higher proportion of the large-bodied piscivorous murres and puffins, compared with the small-bodied planktivorous auklets and storm-petrels (Appendix 4).

Although more seabirds inhabit the EBS, the GOA supports more seabird colonies (i.e., 1,120 versus 472 respectively) (USFWS 2004). Consequently, seabird colonies are larger in the EBS than in the GOA. The median colony size of the EBS (463 individuals) is over 4 times greater than the GOA (103 individuals) (Table 1). The largest colony in the EBS, Buldir Island, is located in the Aleutian Islands with over 3.5 million birds. The largest colony complex in the GOA is the Semidi Islands with a breeding population of nearly 1.5 million birds (USFWS 2004).

The EBS has a total foraging area of 942,552 km^2 and the GOA has a total foraging area of 549,763 km^2 (Table 1) (Fig. 1). Hence, the total density of seabirds in the EBS (21.6 km^{-2}) is less than twice as much as in the GOA (13.0 km^{-2}). The seabird biomass density is similar in the two regions: 7219 g km^{-2} in the EBS and 6689 g km^{-2} in the GOA, (Table 2).

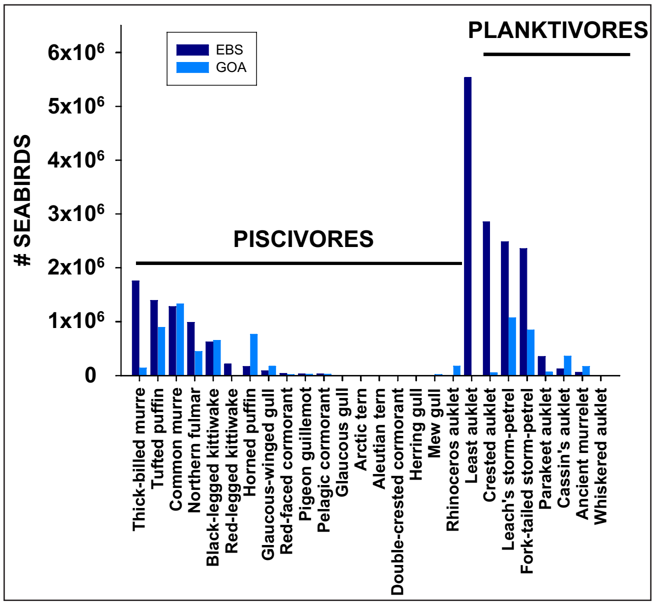

Fig. 4. Population size piscivorous and planktivorous seabird species in the eastern Bering Sea and Gulf of Alaska (USFWS 2003).

TABLE 2

Seabird population and biomass density, per km^2 in the eastern Bering Sea (EBS) and Gulf of Alaska (GOA) for piscivores and planktivores (Hunt *et al*. 2000, USFWS 2004).

	Seabird Population/km^2		**Seabird Biomass/km^2**	
Guild	**EBS**	**GOA**	**EBS**	**GOA**
Piscivorous	7.6	8.4	6.124	6.295
Planktivorous	14.6	4.6	1.666	.394
All Species	22.2	13.0	7.790	6.689

DISCUSSION

Ocean productivity appears to be higher in the EBS than in the GOA. The Bering Sea is considered one of the world's most biologically productive environments (Beringia Conservation Program, National Research Council 1996 and World Wildlife Fund 2001). Regions of high primary productivity occur at upwellings at the edge of the continental shelf, Aleutian Islands arc, and along the GOA mainland (Springer *et al*. 1989, Springer & McRoy 1993). Annual primary production in the GOA has been estimated to be as high as 300 gC m^{-2} in Lower Cook Inlet and the Kenai shelf (Sambrotto & Lorenzen 1987). In the EBS, annual primary production has been estimated to be as high as 300 gC m^{-2} along the Aleutian Islands, 365 gC m^{-2} along the continental shelf break, and up to 800 gC m^{-2} in the Anadyr Stream across the Bering-Chukchi shelf in the northern Bering Sea and southern Chukchi Sea (Springer & McRoy 1993). Generally, phytoplankton and zooplankton biomass levels in the Bering Sea are higher than those of the central and eastern sub arctic Pacific (Sugimoto and Tadokoro 1997). From 1980 to 1994, zooplankton biomass was on average 1.7 times higher and chlorophyll concentration 1.4 times higher in the EBS than in GOA (Sugimoto & Tadokoro 1997) (Table 1).

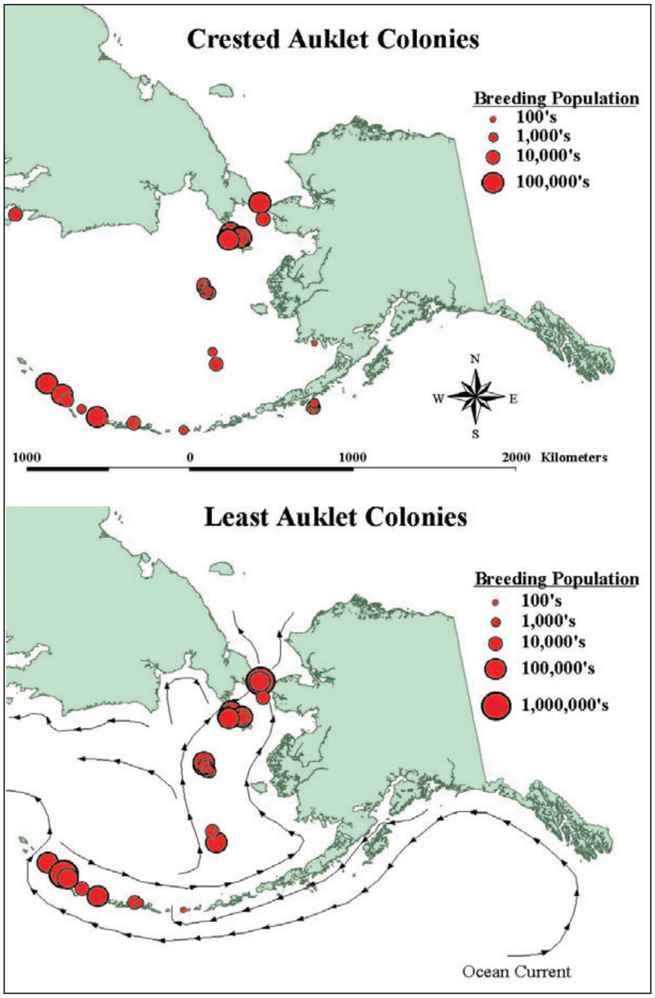

Fig. 5. Location and size of Crested and Least Auklet colonies (with breeding populations >100) and ocean currents in Alaska (Stabeno *et al*. 2003, USFWS 2004).

Groundfish are also more abundant in the EBS than in the GOA. The EBS produces nearly 5 times the amount of groundfish as the GOA (19.8 versus 4.0 million metric tons, respectively) (Table 1) (NMFS unpublished). In addition, the groundfish catch in the EBS, 1.8 million metric tons in 2002, is much higher than in the GOA, 166 000 metric tons in 2002 (NMFS unpublished).

We suggest that the higher numbers of seabirds in the EBS compared to the GOA is partly due to the EBS being larger than the GOA and partly due to the presence of millions of small colonial planktivorous auklets that occur in the EBS but not in the GOA. There is evidence that two factors may contribute to the auklets limited distribution; the availability of quality nesting habitat and areas rich in their food resources.

Least Auklets and Crested Auklets, the two most numerous breeding seabird species in Alaska, nest at 45 and 39 colonies, respectively (Fig. 5). All are located on volcanic islands, most of which are in the Bering Sea (Biekman 1994, USFWS 2004). The northern Bering Sea Islands are older volcanic islands and nearly all of the Aleutian Islands are relatively young (< 2 million years old) volcanic rock, largely basalt pyroclastic lava flows and volcaniclastic debris (Biekman 1994). Moreover, volcanic activity continues in the Aleutians: at least 29 volcanic centers had eruptions and 12 additional volcanic centers may have had eruptions since 1760 (Miller *et al*. 1998). The GOA on the other hand is characterized by very little volcanic rock close to the shoreline. Bedrock is approximately 40 to 70 million years old and is mainly sedimentary, including sandstone, shale, and mudstone (C. Neal, pers. comm.). There are only 7 very small Crested and 1 tiny Least Auklet colonies in the GOA, all situated on the few islands of volcanic origin (Biekman 1994, USFWS 2004). However, while the correlation of volcanic islands and nesting auklets fit relatively well, the eastern Aleutians form an exception, having no auklets despite recent volcanic activity. This scarcity of auklets may be due to a lack of suitable colony sites close to upwelling areas (J. Piatt, pers. comm).

The distribution of Crested and Least Auklet colonies among the volcanic islands in the Bering Sea appears to be determined by ocean productivity and prey availability. These dominant species of planktivores flourish in areas with high zooplankton concentrations on the edge of upwelling and frontal zones (Hunt *et al*. 1993, Stabeno *et al*. 2003, USFWS 2004) (Fig. 5). During summer, high concentrations of nutrients and plankton from the Bering Sea shelf edge are advected north over 1200 km to the central Chukchi Sea and provide a conveyor belt of abundant food to huge seabird colonies in the northern Bering Sea (Piatt & Springer 2003). The western and central Aleutians have areas of upwelling and high productivity that provide food for the largest colonies of auklets (Springer *et al*. 1996).

Least and Crested Auklets are absent from the volcanic islands in the eastern Aleutians. The reason for this void may lie in the type of water that surrounds these islands. The Alaska Coastal Current flows west along the GOA down the Alaska Peninsula and into the Bering Sea through eastern passes. Recent studies have shown that this relatively warmer, fresher water flows west as far as Samalga Pass, the end of the contiguous continental shelf, between Umnak Island and the Islands of Four Mountains. The water to the west of Samalga Pass is colder, saltier, oceanic water (C. Ladd unpublished). Samalga Pass is beginning to be recognized as a biogeographic break in the Aleutian Islands, the distributions of benthic species such as the sunflower star *Pycnopodia helianthoides* and bull kelp *Neroecystis luetkeana* which are common in the GOA end there (J. A. Estes, pers. comm.). Steller sea lion *Eumetopias jubatus* diets are similar throughout the western and central Aleutians, but change dramatically at Samalga Pass (Sinclair & Zeppelin 2002). All of the auklet colonies in the Aleutians are west of Samalga Pass. Hunt *et al*. (1990) found that Least Auklets avoided the warmer, fresher Alaska Coastal Current water near King Island to forage in colder, saltier oceanic water. Another recent study showed that Short-tailed Shearwaters *Puffinus tenuirostris* and Northern Fulmars *Fulmarus glacialis* consumed different prey in passes in the eastern and central Aleutians. Birds east of Samalga Pass ate more shelf break euphausiids than those in the central Aleutians which ate more oceanic copepods. Salmaga Pass may be an east-west divide between two distinct marine environments in the Aleutian Islands (J. Jahncke unpublished) and the marine environment east of Salmaga Pass may not have the dense concentrations of oceanic copepods and euphausiids that support huge auklet colonies.

High quality auklet nesting habitat may be available for only relatively few years on islands in the lower latitudes of their range. Planktivorous auklet species nest in crevices within talus slopes with broken, fragmental, blocky rock deposits. As the talus ages, vegetation forms over the rocks and covers the crevice or openings to nest sites, possibly limiting the availability of favorable nest sites (I. Jones, pers. comm). A photograph taken of a historical site of a large auklet colony at Sirius Point, Kiska Island, in the 1940s shows much of the area was unvegetated lava flow. In 2002, biologists visiting Sirius Point found the area to be highly vegetated and devoid of nesting auklets because of inaccessibility to rock crevices (I. L. Jones, pers. comm). Instead, auklets nested nearby in an unvegetated lava flow formed in 1962 (Miller *et al*. 1998). Vegetation growth appears to be more of a factor in limiting nesting auklets in the Aleutian Islands and GOA than on islands in the northern Bering Sea. Most volcanic rock auklet nesting areas on Saint Lawrence and Little Diomede Island are very old (cretaceous and tertiary period), yet there is little vegetative cover, presumably because of the severe climate at that latitude. These observations suggest that substrate age and type may play an important part in determining the locations of Crested and Least Auklet colonies in Alaska.

If productivity is higher in the EBS, why is seabird biomass density similar between the two regions? Springer (1991) suggested that auklet populations may be limited by competition for food with juvenile Pollock. We suggest another possibility: predation. Predators affect seabird distribution and abundance in Alaska. In the Bering Sea, foxes exist naturally on the northern islands, the sea freezes and provides access to the islands during winter. Foxes are also indigenous to the Fox Islands in the eastern Aleutian Islands, they have apparently been there since the Pleistocene, when the islands were connected to the mainland by ice or land bridges (Bailey 1993). In the GOA, foxes are indigenous only to a few large islands. Most islands in the central and western Aleutians and in the GOA were naturally fox free. However, foxes were introduced to more than 450 islands in Alaska from 1750 to the 1930s for fur farming. Islands with large seabird populations were often specifically chosen for introductions so that the foxes would have a ready food source. These foxes decimated burrow- and surface-nesting seabird populations on many of the islands (Bailey 1993). Today, introduced foxes have been eradicated or have naturally died off most islands in the GOA and many islands in the Aleutians (Williams *et al*. 2003). The seabirds are starting to recover, but several populations in the western and central Aleutians are still depressed (Bailey 1993). Interestingly, the two largest mixed species seabird colonies in the Aleutians are on Buldir and Chagulak Islands (USFWS 2004), two islands where foxes were never introduced. The impact of fox predation on seabirds has been greater in the EBS than in the GOA, both because of more islands with indigenous foxes and more successful introductions in the EBS. Predation by foxes, both indigenous and introduced, may be part of the reason that there are not more seabirds in the EBS.

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REFERENCES

AGLER, B.A., KENDALL, S.J., IRONS, D.B., & KLOSIEWSKI, S.P. 1999. Declines in Marine Bird Populations in Prince William Sound, Alaska Coincident with a Climatic regime Shift. *Waterbirds* 22: 98-103.

ANDERSON, P.J. & PIATT, J. F. 1999. Community reorganization in the Gulf of Alaska following ocean climate regime shift. *Marine Ecology Progress Series* 189: 117-123.

ASHMOLE, N.P. 1963. The regulation of numbers of tropical oceanic seabirds. *Ibis* 103b: 458-473.

BAILEY, E.P. 1993. Introduction of foxes to Alaskan islands-history, effects on avifauna, and eradication. U.S. Dept. of the Interior, Fish and Wildlife Service Resource Publication 193.

BEIKMAN, H. 1994. Geologic map of Alaska. In: Plafker, G. & Berg, H.C. (Eds.). The Geology of Alaska, Geological Society of America, The Geology of North America, v. G-1, plate 1.

BERINGIA CONSERVATION PROGRAM & WORLD WILDLIFE FUND. 2001. The Bering Sea ecoregion; a call to action in marine conservation. World Wildlife Fund Public Information Report: pp 32.

BIRKHEAD, T.R. & FURNESS, R.W. 1985. The regulation of seabird populations. In: Sibly R.M. & Smith R.H. (Eds.), Behavioral Ecology. Blackwell, Oxford, pp. 145-167.

BROWN, J.H. & LOMOLINO, M.V. 1996. Biogeography. Sinauer Associates. Sunderland, Mass.

DEGANGE, A.R., DAY, R.H., TAKEKAWA, J.E. & MENDENHALL, V.M. 1993. Losses of seabirds in gill nets in the North Pacific. In: Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds.). The status, ecology, and conservation of marine birds of the North Pacific. Ottawa: Environment Canada. pp. 204-211.

FURNESS, R. & MONAGHAN, P. 1987. Seabird ecology. Chapman and Hall. New York, New York.

GASTON A.J. & HIPFNER, J.M. 2000. Thick-billed Murre (*Uria lomvia*). In: Poole, A. and Gill, F. (Eds.). The Birds of North America, No. 497. The Birds of North America, Inc., Philadelphia, PA.

HATCH, J.J. 2002. Arctic Tern (*Sterna paradisaea*). In: Poole, A. & Gill, F. (Eds.). The Birds of North America, No. 707. The Birds of North America, Inc., Philadelphia, PA.

HUNT, J.L., JR., HARRISON, N.M. & COONEY, R.T. 1990. The influence of hydrographic structure and prey abundance on foraging of least auklets. *Studies in Avian Biology* 14: 7-22.

HUNT, J.L., JR., HARRISON, N.M. & PIATT, J.F. 1993. Foraging ecology as related to the distribution of planktivorous auklets in the Bering Sea. . In: Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds.). The status, ecology, and conservation of marine birds of the North Pacific. Ottawa: Environment Canada. pp. 18-26.

HUNT, J.L., JR., HIDEHI, O.K. & MCKINNEL, S.M. 2000. Predation by marine birds and mammals in the North Pacific Ocean. PICES Scientific Report No. 14 2000, North Pacific Marine Science Organization.

LACK, D. 1966. Population studies of birds. Oxford University Press, Oxford.

LENSINK, C.J. 1984. The status and conservation of seabirds in Alaska, In: Croxall, J.P., Evans, P.G.H. & Schreiber, R.W. (Eds.). Status and Conservation of the World's Seabirds, Cambridge: International Council for Bird Preservation. pp 13-28.

MILLER, T.P., MCGIMSEY, R.G., RICHTER, D.H., RIEHLE, J.R., NYE, C.J., YOUNT, M.E. & DUMOULIN, J.A. 1998. Catalog of the historically active volcanoes of Alaska. Open File Report 98-582, U.S. Geological Survey, Anchorage, Alaska and Alaska Division of Geological and Geophysical Surveys, Fairbanks, Alaska.

NATIONAL RESEARCH COUNCIL. 1996. The Bering Sea ecosystem: geology, physics, chemistry, and biology of lower trophic levels. National Academy Press, Washington D.C. Chapter 3, pp 28-71.

PIATT, J. F., LENSINK, C. F., BUTLER, W., KENDZIOREK, M. & NYSEWANDER, D. R. 1990. Immediate impact of the 'Exxon Valdez' oil spill on marine birds. *Auk* 107:387-397.

PIATT, J.F. & SPRINGER, A.M. 2003. The paradox of pelagic food webs in the northern Bering Sea—IV: Seabird Biogeography. *Marine Ornithology* 31: 141-154.

SAMBROTTO, R.N. & LORENZEN, C.J. 1986. Phytoplankton and primary production. In: Hood, D.W. & Zimmerman, S.T. (Eds.). The Gulf of Alaska; Physical Environment and Biological Resources. U.S. Departments of Commerce and the Interior, Minerals Management Service Publ. OCS Study MMS 86-0095. pp 249-282.

SINCLAIR, E.H. & ZEPPLIN, T.K. 2002. Seasonal and spatial differences in diet in the western stock of Steller sea lions (*Eumetopias jubatus*). *Journal of Mammology* 83: 973-990.

SOWLS, A.L., HATCH, S.A. & LENSINK, C.J. 1978. Catalog of Alaskan seabird colonies. U.S. Fish and Wildlife Service, Biological Services Project, FWS/OBS-78/78.

SPRINGER, A.M. 1991. Seabird distribution as related to food webs and the environment: examples from the north Pacific Ocean. In: Montevecchi, W.A. & Gaston, A.J. (Eds.). Studies of High Latitude Seabirds 1: Behavioral, Energetic and Oceanographic Aspects of Seabird Feeding Ecology. Canadian Wildlife Service Occasional Paper No 68, Canadian Wildlife Service, Ottawa: pp. 39-48.

SPRINGER, A.M. & MCROY, C.P. 1993. The paradox of pelagic food webs in the northern Bering Sea - III. Patterns of primary production. *Continental Shelf Research* 13: 575-599.

SPRINGER, A.M., MCROY, C.P. & TURCO, K.R. 1989. The paradox of pelagic food webs in the northern Bering Sea - II. Zooplankton communities. *Continental Shelf Research* 9: 359-386.

SPRINGER, A.M., PIATT, J.F. & VAN VLIET, G. 1996. Seabirds as proxies of marine habitats in the western Aleutian arc. *Fisheries Oceanography* 5:45-55.

STABENO, P.J., SCHUMACHER, J.D. & OHTANI, K. 2003. The physical oceanography of the Bering Sea. In: Laughlin, T.R. & Ohtani, K. (Eds.). Dynamics of the Bering Sea: a summary of physical, chemical, and biological characteristics, and a synopsis of research on the Bering Sea. North Pacific Marine Science Organization (PICES), University of Alaska Sea Grant, AK-SG-99-03, pp. 1-28.

STEPHENSEN, S.W. 2001. The Beringian Seabird Colony Catalog Annual Report. Unpublished Report, U.S. Fish and Wildlife Service, Anchorage, Alaska. 26 pp.

STEPHENSEN, S.W. & MENDENHALL, V.M. 1998. Alaska Seabird Recensus Plan. Unpublished Report, U.S. Fish and Wildlife Service, Anchorage, Alaska. 153 pp.

SUGIMOTO, T. & TADOKORO, K. 1997. Interannual-interdecadal variations in zooplankton biomass, chlorophyll concentration and physical environment in the subarctic Pacific and Bering Sea. *Fisheries Oceanography* 6: 74-93.

UDVARDY, M.D.F. 1976. Did Santa Rosalia like sea-birds? Proceedings of the 16th International Ornithological Congress, August 1974. Australian Academy of Science Canberra City, A.C.T. 2601, Australia.

U.S. FISH & WILDLIFE SERVICE. 1992. Alaska Seabird Management Plan. Unpublished Report, U.S. Fish and Wildlife Service, Anchorage, Alaska. 102 pp.

U.S. FISH & WILDLIFE SERVICE. 1994. Seabird Colony Catalog: manual for interpretation of colony data for data entry. U.S. Fish and Wildlife Service Manual, Migratory Bird Management. Anchorage, Alaska. 33 pp.

U.S. FISH &WILDLIFE SERVICE. 1999. Beringian Seabird Colony Catalog manual for censusing seabird colonies. U.S. Fish and Wildlife Service Report, Migratory Bird Management. Anchorage, Alaska. 27 pp.

U.S. FISH &WILDLIFE SERVICE. 2004. Beringian Seabird Colony Catalog--computer database and Colony Status Record archives. U.S. Fish and Wildlife Service, Migratory Bird Management, Anchorage, Alaska 99503.

WILLIAMS, J.C., BYRD, G.V. & KONYUKHOV, N.B. 2003. Whiskered Auklets *Aehtia pygmaea*, foxes, humans and how to right a wrong. *Marine Ornithology* 31: 175-180.

Appendix 1

Seabird species, breeding population and number of colonies in the Eastern Bering Sea (EBS) and Gulf of Alaska (GOA), and number of colonies that contain 50% of the total species population (USFWS 2004). Foraging guilds according to Gaston and Hipfner (2000), Hatch (2002), Hunt et al. (2000). Biomass from Hunt et al. (2000), USFWS (2003)

Species	Foraging guild	Number of colonies		Population		Colonies with 50% of species population	Body Mass (kg)*	Biomass (kg)	
		EBS	GOA	EBS	GOA			EBS	GOA
Northern Fulmar *Fulmarus glacialis*	Pisc.	22	16	983,983	440,217	2	0.544	535,287	239,478
Fork-tailed Storm Petrel *Oceanodroma furcata*	Plank.	56	56	2,354,806	840,530	2	0.0553	130,221	46,481
Leach's Storm Petrel *Oceanodroma leucorhoa*	Plank.	51	43	2,483,392	1,067,952	2	0.0398	98,839	42,504
Double-crested Cormorant *Phalacrocrax auritus*	Pisc.	34	72	2,668	3,400	7	1.674	4,466	5,692
Pelagic Cormorant *Phalacrocorax pelagicus*	Pisc.	173	214	24,184	19,257	15	1.868	45,176	35,972
Red-faced Cormorant *Phalacrocorax urile*	Pisc.	91	122	33,616	13,877	10	2.157	72,510	29,933
Mew Gull *Larus canus*	Pisc.	3	65	234	14,135	4	0.4035	94	5,703
Herring Gull *Larus argentatus*	Pisc.	22	13	861	706	4	1.135	977	801
Glaucous-winged Gull *Larus glaucescens*	Pisc.	223	592	85,199	167,036	42	1.01	86,051	168,706
Glaucous gull *Larus hyperboreus*	Pisc.	63	0	5,680	0	7	1.4125	8,023	0
Black-legged Kittiwake *Rissa tridactyla*	Pisc.	100	249	619,081	648,858	16	0.407	251,966	264,085
Red-legged Kittiwake *Rissa brevirostris*	Pisc.	7	0	208,851	0	1	0.391	81,661	0
Arctic Tern *Sterna paradisaea*	Pisc.	33	114	2,840	7,599	14	0.11	312	836
Aleutian Tern *Sterna aleutica*	Pisc.	34	22	2,770	6,793	3	0.12	332	815
Common murre *Uria aalge*	Pisc.	140	90	1,505,849	1,326,793	7	0.9925	1,494,555	1,316,842
Thick-billed Murre *Uria lomvia*	Pisc.	121	53	2,071,438	134,171	1	0.964	1,996,866	129,341
Pigeon Guillemot *Cepphus columba*	Pisc.	237	643	25,867	23,090	39	0.487	12,597	11,245
Ancient Murrelet *Synthliboramphus antiquus*	Plank.	43	47	54,363	164,403	3	0.206	11,199	33,867
Cassin's Auklet *Ptychoramphus aleuticus*	Plank.	22	30	118,090	354,853	3	0.188	22,201	66,712
Least Auklet *Aethia pusilla*	Plank.	35	2	5,528,743	20	5	0.084	464,414	2
Parakeet Auklet *Cyclorhynchus psittacula*	Plank.	88	107	349,181	57,992	3	0.258	90,089	14,962
Whiskered Auklet *Aethia pygmaea*	Plank.	44	0	6,712	0	2	0.121	812	0
Crested Auklet *Aethia cristatella*	Plank.	36	7	2,851,955	46,050	4	0.264	752,916	12,157
Rhinoceros Auklet *Cerorhinca monocerata*	Pisc.	1	18	30	170,065	1	0.52	16	88,434
Tufted Puffin *Fratercula cirrhata*	Pisc.	248	445	1,389,380	888,864	15	0.779	1,082,327	692,425
Horned Puffin *Fratercula corniculata*	Pisc.	217	391	160,513	760,265	4	0.619	99,358	470,604
TOTALS	Pisc.			7,123,044	4,625,126			5,772,574	3,460,912
	Plank.			13,747,242	2,531,800			1,570,691	216,686
	All Species			**20,870,286**	**7,156,926**			**7,343,265**	**3,677,598**

WHISKERED AUKLETS *AETHIA PYGMAEA*, FOXES, HUMANS AND HOW TO RIGHT A WRONG

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SUMMARY

WILLIAMS, J.C., BYRD G.V. & KONYUKHOV, N.B. Whiskered Auklets *Aethia pygmaea*, foxes, humans and how to right a wrong. *Marine Ornithology* 31: 175-180

Whiskered Auklets *Aethia pygmaea* forage exclusively on zooplankton concentrated in tiderips, swirls, tidal pumps and fronts of strong upwelling near islands or offshore reefs. This foraging habitat, which is common throughout the Aleutian and Kurile islands, is the primary factor determining the biogeography of Whiskered Auklets. Arctic Foxes *Alopex lagopus* were first introduced to nearly all of these islands devoid of terrestrial predators as early as the mid-1700's. Introductions reached their peak from 1913 to 1940 and were successful because foxes preyed on the native seabird populations. By 1940 at least 90 islands had non-native Arctic Foxes introduced, and there were thought to be only a few thousand Whiskered Auklets in the Aleutian Islands. The staff of the Aleutian Islands reservation (now part of the Alaska Maritime National Wildlife Refuge) started eradicating foxes from refuge islands in 1949. By 1974 the Whiskered Auklet Aleutian Island population was estimated to be approximately 25 000 individuals. By 2002, foxes had been removed from 40 islands (restoring 1800 miles of nesting coastline) and remained on only 6 islands. We estimate that by 2003 there were at least 116 000 Whiskered Auklets throughout the Aleutians Islands, widely distributed in formerly occupied nesting areas. Almost uniquely among alcids, many young and adult Whiskered Auklets return to the breeding colony after fledging to sleep on the surface of boulders at nesting colonies. This behavior disposed Whiskered Auklets to excessive predation relative to other crevice-nesting species that were thought to be safe nesting under boulders. We summarize evidence suggesting that Whiskered Auklets were abundant prior to fox introductions, experienced large declines at the peak of fur farming, and are now recovering to former levels after an active fox removal program. We argue that the introduction of non-native Arctic Foxes has regulated the distribution and abundance of Whiskered Auklets for the last 250 years.

Keywords: Whiskered Auklet, *Aethia pygmaea*, population regulation, Aleutian Islands, Arctic fox, predation, roosting

INTRODUCTION

Whiskered Auklets *Aethia pygmaea* are relatively rare alcids, currently distributed on select islands within the Aleutian, Commander, and Kurile island chains of the North Pacific to which they are endemic (Fig. 1; Byrd & Williams 1993, Gaston & Jones 1998). Whiskered Auklets forage in tiderips, swirls, and tidal pumps or fronts on zooplankton that is concentrated near islands and offshore reefs by strong upwelling (Byrd & Gibson 1980, Byrd & Williams 1993, Gaston & Jones 1998). These foraging areas are persistent in space and time and largely do not depend on the season (Zubakin & Konyukhov 2001). Because of this, Whiskered Auklets are mostly non-migratory, unlike other *Aethia* species, and are found year-round within 16 km of shore (Byrd & Gibson 1980). This nearshore marine foraging habitat is common throughout the Aleutian and Kurile islands, and is the primary factor regulating the distribution and abundance of Whiskered Auklets (Zubakin & Konyukhov 2001).

During the 18th, 19th, and 20th centuries, fur trappers introduced Arctic Foxes *Alopex lagopus* into this region, for the purpose of fur farming, which caused substantial reductions in populations of native birds (Dall 1873, Snow 1897, Murie 1936, Bailey 1993). Whiskered Auklets and other seabird species that nest in rock crevices were expected to be less affected by fox predation than species that nest on the ground or in earthen burrows (Bailey 1993). However, historical accounts of Whiskered Auklet distribution and abundance suggest this has not been the case (Dall 1873, Snow 1897, Murie 1936, 1937).

Until recently, little was known about the biology of the Whiskered Auklet. The earliest directed research documented distribution (Byrd & Gibson 1980), breeding biology (Knudtson & Byrd 1982), and food habits (Day & Byrd 1989), but all these studies were hampered by small sample sizes or were based on only a single year of data. Recent multi-year research has shed new light on courtship behavior (Hunter & Jones 1999), food habits (Hunter *et al*. 2002), molt (Konyukhov 2001, Pitoccelli *et al*. 2003), and breeding biology (Konyukhov & Zubakin 1994, Zubakin & Konyukhov 1999, 2001, Hunter *et al*. 2002). Based on some of these studies, we now know that in spite of nesting in rock crevices, Whiskered Auklets are particularly predisposed to predation by Arctic Foxes due to their unique biological characteristics within the *Aethia* family.

Originally the management of Arctic Foxes began with the objective of maximizing fur production, a practice that resulted in the exploitation of the insular avifauna, including Whiskered Auklets. Anecdotal accounts described decimated bird populations in the early 18th century (Dall 1873, Black 1984). Directed surveys by Olaus Murie in the 1930's (Murie 1936, 1937) helped changed the management policy from one of exploitation and decimation of the avifauna to one of conservation. In this paper, we summarize evidence suggesting that Whiskered Auklets were abundant prior to fox introductions, experienced large declines at the peak of fur farming, and are now recovering to former levels after the onset of an active fox removal program. Furthermore, we argue that the introduction of these non-native Arctic Foxes has regulated the distribution and abundance of Whiskered Auklets for the last 250 years.

"Foxes come, birds go"

The Aleutian Islands have no native terrestrial mammals west of Umnak Island (Buskirk & Gipson 1980, Bailey 1993). Widespread introductions of Arctic Foxes began on Attu Island in 1750 by some of the first Russian traders in the region (Black 1984). Foxes were steadily introduced to new islands throughout the 1800s during the period of Russian occupation. Once introduced into this pristine environment, foxes prospered on the abundant birds that had evolved free of terrestrial predators. Fox farmers regarded seabirds simply as food for foxes (Bailey 1993). Islands that produced the most foxes were those which historically supported the largest number of birds -primarily seabirds (Alaska Maritime National Wildlife Refuge administrative files).

Not long after these initial fox introductions, early naturalists noted major changes in this remote environment. Naturalist William Dall (1873, p. 271) noted:

> "…on those islands such as Attu and Atka, where the arctic fox and other land animals have been introduced by the Russians, the birds preferred to build on islets and rocks offshore, or not accessible from the beaches. But on those islands where there are no such animals, the habits of the same species are quite different. They build without fear, on the banks and hillsides of the main island, and are not found on the rocky islets at all."

By 1812, less than 60 years after foxes were introduced to Attu, birds were described as rare there and the native Aleuts were making clothing from fish instead of birds (Black 1984). On Amlia Island, the decline of avifauna after fox introduction was even more rapid. By 1811, only 20 years after fox introduction to this island, native Aleuts complained that foxes had driven away the birds which were formerly abundant and upon which they depended for food and clothing (Black 1984, Bailey 1993).

After Alaska was sold to the United States in 1867, the Secretary of the Treasury began formal leasing of Alaskan islands for fur farming in 1882; this practice continued for the next 60 years (Bailey 1993). Fox introductions to new islands reached a peak from 1913 (after the area was designated as the Aleutian Islands Reservation – precursor to the Alaska Maritime National Wildlife Refuge) to 1940 (when nearly every island had had non-native Arctic Foxes introduced). In 1921, at least 23 Aleutian Islands were under permit to fox farming operations, and by 1931 over 86 islands were permitted. Additional islands were illegally stocked with foxes or no records exist of their introduction to those islands (Bailey 1993).

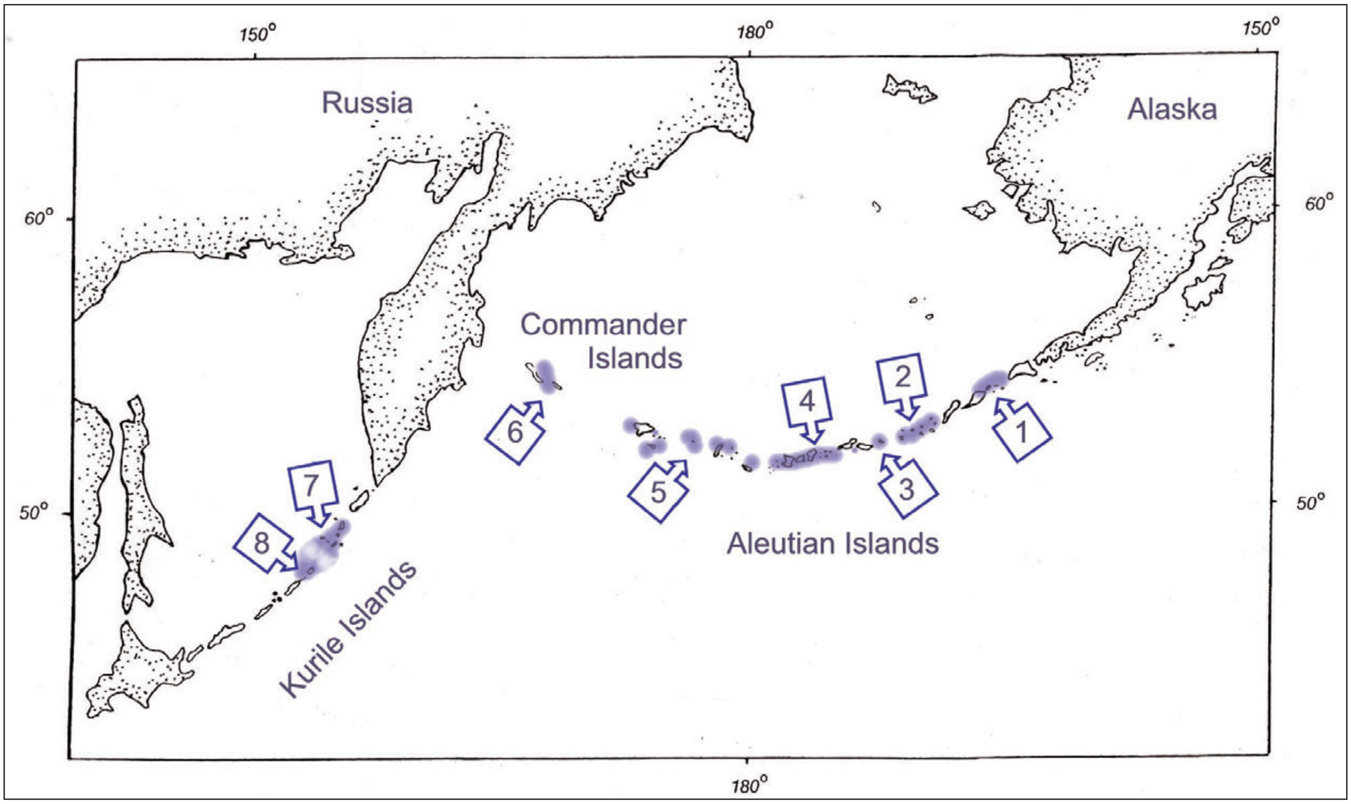

Fig. 1. Map of the North Pacific showing major Whiskered Auklet concentration sites (arrows) and generalized areas of strong tidal currents (shaded). Numbered squares refer to (1) Eastern Aleutian Islands (including Baby Pass), (2) Islands of 4 Mountains, (3) Seguam Island, (4) Central Aleutian Islands (including Kanaga, Great Sitkin, Ulak, Kasatochi, Koniuji, and Amlia Islands), (5) Buldir (including Kiska to the east and Near Islands to the west), (6) Commander Islands, (7) Northern Kuril Islands, (8) Central Kuril Islands: based on information in Zubakin and Konyukhov (2001).

By the mid 1930s there were clear and serious conflicts between fox farming and the preservation of the Aleutian avifauna. In 1936, the Biological Survey (later to become the U.S. Fish and Wildlife Service) dispatched Olaus Murie and several biologists to investigate the situation "with a view to obtaining all possible information on which to form a basis for effective management of the Aleutian Islands Reservation" (Murie 1936, p.1). One of the people accompanying Murie was Douglas Gray, deputy Alaska game warden and future Refuge Manager, who summed up how dark the situation had become for the avifauna of the Aleutians:

> "It was found that 99% of the total acreage [2 868 320 acres] was used for fox propagation purposes. ...*The entire refuge was operating for one purpose: fox farm production* [italics added]. No concern or protection was granted the various forms of wildlife inhabiting the refuge… In many cases, bird colonies were completely cleaned off as their numbers were too small to survive the depredations of the foxes. In the others, there is no way to determine how much wildlife has suffered. The natives sum up the situation with the terse remark 'foxes come, birds go' ". (Gray 1939, p. 2)

The speed and extent to which foxes altered the abundance and distribution of avifauna appear to have depended on island size and the species composition of the breeding seabird populations (Murie 1936, 1937, 1959). The larger the island or colony size, the longer it took to reduce bird numbers. Only the largest colonies were thought to be able to withstand the intense predation pressure by foxes (Murie 1937). Smaller islands with fewer birds fared poorly. Burrowing species such as Tufted Puffin *Fratercula cirrhata*, Leach's and Fork-tailed Storm-petrels *Oceanodroma leucorhoa* and *O. furcata*, Cassin's Auklet *Ptychoramphus aleuticus*, and Ancient Murrelet *Synthliboramphus antiquus* rapidly disappeared because they could easily be excavated from their burrows by foxes (Bailey 1993).

Based on the reports of Murie (1936, 1937) and Gray (1939) the Biological Survey changed the manner in which many of the islands were managed and designated some as wildlife sanctuaries and others to remain as fox farms. In the late 1930's the primary fox food source had become so depleted that most fox farmers were forced into supplemental feeding to make trapping economically feasible (Bailey 1993). During World War II, all civilians, including trappers, were evacuated and fox farming was abandoned as Japanese and American forces battled in the region. After the war, the fox farming business had become unprofitable because demand for pelts in the fashion industry significantly diminished. As a result most fox farm leases lapsed or were abandoned. However, the abandoned foxes remained on the islands eating birds and anything else they could find.

"Foxes go, birds come"

In 1949, Bob Jones, refuge manager of the Aleutian Islands Reservation, recognized the damage caused by introduced Arctic Foxes, and began eradicating foxes on Amchitka Island using traps and poison. This marked a significant change in management policy from one of exploitation to one of conservation (Bailey & Kaiser 1993). Later, environmental legislation and institutional changes formalized this approach (Sekora 1973). Removal of foxes from islands continued slowly but steadily until the 1970s, when the effort and funding allocation increased and foxes were eradicated from approximately one island per year (Ebbert 2000, Ebbert & Byrd 2002). Foxes had naturally died off on a number of small islands where foxes had completely eradicated the native avifauna (Bailey 1993, Ebbert 2000). By 2002, the refuge had removed foxes from 40 islands, restoring approximately 2880 km of coastline and 4047 km^2. Today, foxes remain on only 6 of the Aleutian Islands (Shemya, Tanaga, Kanaga, Adak, Atka, Chuginadak) to which they were introduced, and the region is returning to the conditions that existed prior to the human introduction of Arctic Foxes (Ebbert 2000). Tufted Puffins and other seabirds have dramatically increased in abundance and changed their nesting distribution from formerly fox-inaccessible offshore islets and rocks, to large islands (Byrd *et al*. 1994). Species such as Rock Ptarmigan *Lagopus mutus*, Aleutian Canada Geese *Branta canadensis leucopareia* and other waterfowl have also responded dramatically to the fox removal (Byrd *et al*. 1994).

Effects on Whiskered Auklet biogeography

There are only a few accounts from which to recreate the early historic abundance of Whiskered Auklets, but they provide a glimpse of the situation at a time when most fox introductions were just beginning. The naturalist Lucien Turner reported Whiskered Auklet as "quite abundant" in the Near Islands group of the Aleutians and "common" at locations in the central Aleutians in 1879 (Turner 1886). Snow (1897, p. 10 & 30) described Whiskered Auklet abundance in the Kurile Islands:

> "…whilst millions of little auks, of several species (*Phaleris cristatella* [Crested auklet] and *P. mystacea* [Whiskered Auklet] being the most common)… large numbers of these auks [breed] on all the islands…"

Leonhard Stejneger (1885, p. 31) described Whiskered Auklets in the Commander Islands as "rather common". However, Stejneger noted that an observer would need "good luck" to encounter the species even though they were common. Most likely this was because Whiskered Auklets are seldom found outside their preferred foraging places in rip tides and fronts off points close to land (Byrd & Gibson 1980, Byrd & Williams 1993) – treacherous places early sailing ships avoided for obvious reasons. After these observations, foxes were continually introduced to many of the Aleutian Islands.

In 1911, A.C. Bent (1919) spent several weeks in the Aleutians surveying for Whiskered Auklets throughout the island chain, but failed to observe a single specimen. No other descriptive accounts of Whiskered Auklet abundance exist until 1936, when fox introductions to islands were at their peak. Olaus Murie (1936) noted that Whiskered Auklets had disappeared from the Near Islands where they were once abundant and were becoming scarce elsewhere. He estimated that only a few thousand birds bred in the Aleutians at the time. In 1940 and 1946, Gabrielson (1959) considered himself "fortunate" to observe 2 birds throughout his travels in the Aleutians. Clearly, Whiskered Auklets had reached their population nadir just after the peak of fox farming activities. Over the next few decades, foxes died out on some small islands after the native avifauna was extirpated and no food source remained.

The first thorough surveys after Murie's observations were those by Byrd and Gibson (1980), who spent hundreds of hours looking for Whiskered Auklets in 1972-1974. They estimated that there were about 25 000 birds throughout the Aleutians, based on counts of birds at sea. Notably, they observed a single flock of about 10 000 individuals in the Islands of Four Mountains. Other areas of high abundance included Baby Pass in the eastern Aleutians, Seguam Island, and Great Sitkin Island. Additionally a few individuals were observed in the Near Islands.

By 2003, Whiskered Auklets were observed in growing numbers in places such as Agattu Island in the Near Islands where they were formerly "quite abundant" in 1879 (Turner 1886). New nesting records were noted on Kiska, Kanaga, Ulak, Kasatochi, Koniuji and Amlia – all now fox-free. Large numbers of birds were still noted in Baby Pass, Islands of Four Mountains/Yunaska, and Great Sitkin Island. Off Seguam Island, where foxes were removed in 1996, a single flock of whiskered auklets numbering 30 000 – 40 000 was observed – larger than Byrd and Gibson's (1980) population estimate for the entire Aleutian Islands.

We conservatively estimate the current population of Whiskered Auklets throughout the Aleutians to be at least 116 000 individuals distributed as follows: Near Islands – 500; Buldir – 30 000; Kiska to Kanaga – 500; Adak to Atka – 30 000; Seguam – 35 000; Islands of 4-Mountains – 10 000; Umnak to Unimak – 10 000. These estimates, with the exception of Buldir for which we have detailed nesting information, are based on largest counts of birds observed at sea during the breeding season when many individuals were possibly attending nest sites, and should thus be considered minimum estimates.

Why are Whiskered Auklets so vulnerable to predation?

Nearly all seabirds were vulnerable to predation, particularly ground-nesting and burrow-nesting species, when non-native foxes were introduced to the Aleutians, but those nesting in crevices and on cliffs were generally thought to be less susceptible because foxes had greater difficulty gaining access to their nest sites (Murie 1937, Jones & Byrd 1979, Bailey 1993). Whiskered Auklets, however, exhibit several biological characteristics that make them especially vulnerable to foxes compared to other crevice-nesting auklets: low nesting densities, nearly year-round residency, and the return of adults and especially juveniles to sleep on shore after the breeding season. Many of these characteristics likely evolved as a result of competition with other auk species for nest sites (Hunter *et al*. 2002), and due to the proximity of the breeding sites to the nearshore foraging habitat (Zubakin & Konyukhov 2001).

Whiskered Auklets breed at low densities (Hunter *et al*. 2002). When foxes were introduced to islands, Whiskered Auklets lacked the protection afforded by large numbers of the more colonial Crested *Aethia cristatella*, Least *A. pusilla* and, to a lesser extent, Parakeet Auklets *A. psittacula*. Thus, Whiskered Auklets were more easily eradicated from many islands, particularly small ones, once foxes were introduced.

Research in the 1990s (Konyukhov & Zubakin 1994, Zubakin & Konyukhov 2001) indicated that, almost uniquely among alcids, many fledglings return to the breeding colony for at least a month or more after fledging. Nocturnal at the colony, the unwary fledglings can be found sleeping in the open after the breeding season, where they would be easily preyed upon by foxes that patrol beaches at night. It was often easy for Zubakin and Konyukhov to approach these sleeping birds and capture them by hand or small net. Over the years, researchers had often encountered fledgling birds on the ground, apparently disoriented, far inland on islands where they breed (JCW, GVB unpublished data). For instance, Stejneger (1885) found fledglings sleeping in the sail of his ship, Gabrielson (1959) reported fledglings far inland on trails, and Gaston & Jones (1998) documented fledglings 1 km inland. In addition to fledglings returning ashore after the breeding season, Zubakin and Konyukhov (2001) observed substantial numbers of adults sleeping on the surface of the colony after the breeding season. While exposed Whiskered Auklets would be especially vulnerable to fox predation, fledglings of other *Aethia* species are almost never found under these circumstances.

Although these recent observations were the first clear documentation of this behavior, there were earlier hints that Whiskered Auklets visited land after the breeding season. Stejneger (1885) collected birds from shore near a colony in January and thought that Whiskered Auklets spent the night in crevices throughout the year. Similarly, Murie (1936, p. 71) reported that:

> "The natives assured us that this species spends the winter among the Aleutians and that during the season the birds return to their retreats among the rocks to roost, where the foxes get them. Thus due to their roosting habit, these birds fall prey to the foxes year round and suffer much more than the other species [of auklets]. This could well be one of the factors in their present scarcity".

Zubakin and Konyukhov (2001) hypothesized that the return of adults and fledgling birds to land after the breeding season was possible because of the proximity of year round foraging areas. In contrast, other *Aethia* family members disperse to open sea for much of the year (Gaston & Jones 1998).

DISCUSSION

The introduction of Arctic Foxes to the Aleutian Islands had a controlling effect on the distribution and abundance of Whiskered Auklets as a result of their unique biological characteristics, which makes them more vulnerable to predation. Was it a minor effect on population dynamics or was it a driving force that led to near extinction?

Almost 70 years ago Olaus Murie (1936, p. 108) considered the control foxes exerted on seabirds at Kasatochi Island:

> "…as many as 29 foxes have been trapped in a year, with an estimated 24 remaining. If we consider a year with 30 foxes on the island, to be very conservative, and allow these animals to live through a bird nesting season, probably well over 100 days, and allowing only 1 bird a day we would have a loss of over 3000 birds. As a matter of fact, we found in a single cache of one pair of foxes over 100 birds, and none of these were badly decomposed. This in itself would indicate several times the number derived above. The loss of birds by various methods of calculations, such as allowing a cache like the one we found once a week, per pair, and other qualifying estimates, the figures run all the way from

> three to four thousands to as many as 40 000 or even more for the season. The seabirds are prolific and tenacious, but this would be a heavy drain on the population, far in excess of the normal losses."

Some of the seabird colonies in the Aleutians contain more than a million birds of several species, so unless the populations are closely monitored the loss of even 40 000 individuals might go unnoticed. Whiskered Auklets use a wide variety of nesting habitats and historically nested at relatively low densities probably on nearly every island throughout the Aleutian Islands. Murie (1936) stated Aleutian foxes appeared to specialize on certain seabird species and specifically mentioned the Whiskered Auklet as susceptible to predation. The effect of fox predation on seabirds, including Whiskered Auklets, almost certainly depended on how many foxes were present on each island. Little is known about the earliest years of fox farming in the Aleutians because the harvest records were often combined with foxes taken out of the region. However, hundreds of thousands of foxes were harvested during the Russian era (1750-1867) and later (Carnarhan 1979). It wasn't until the early years of the Aleutian Islands Reservation that we get a well-recorded glimpse of the magnitude of the problem. Approximately 27 000 foxes were harvested in the Aleutians from 1913 to 1936 (Jones & Byrd 1979), a time period of diminished returns for foxes because of depleted seabird populations. The actual harvest number was probably higher because not all historical records are available. Because trappers realized the importance of leaving a sufficient breeding stock on each island to ensure future returns, harvested fox pelts represented only a small portion of the total number of foxes preying on seabirds. Nevertheless, even a few foxes could remove large numbers of auklets. Bailey (1993) cited examples where just a few invading foxes killed tens of thousands of nesting birds.

Could the eradication of Arctic Foxes from islands have led to the increases in Whiskered Auklet numbers we have recently observed? We have documented the response of insular Aleutian avifauna after fox eradication since 1975 (Byrd *et al*. 1994, 1997). Increases of up to several hundred percent in just a few years were common as long as there were "seed populations" nearby from which to repopulate the islands. *Aethia* auklets appear to have the ability to rapidly colonize areas of suitable habitat (Gaston & Jones 1998). It is likely that Whiskered Auklets, which remain near potential nesting islands year round and use a wide range of nesting habitats, are capable of responding even more rapidly once released from predation compared to their congeners which require specific breeding substrates (i.e. large talus fields) found in only a few locations. On most islands in the Aleutians we see few impediments to further population increases and range expansion of Whiskered Auklet populations. However, Norway Rats *Rattus norvegicus* have been accidentally introduced to at least 16 islands (Ebbert & Byrd 2002) and may preclude the recovery of Whiskered Auklets and a number of other seabird species.

Unlike many anthropogenic habitat changes, the restoration of native biodiversity has been possible in the Aleutian Islands through an effective eradication program of introduced fox. The management actions resulting from a change in policy from fur production to wildlife conservation has served to right the wrong done to Whiskered Auklets and other native birds in the region.

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REFERENCES

BAILEY, E.P. 1993. Introduction of foxes to Alaskan islands – history, effects on avifauna, and eradication. U.S. Fish and Wildlife Service Resources Publication 193. Washington: U.S. Fish and Wildlife Service.

BAILEY, E.P., & KAISER, G.W. 1993. Impacts of introduced predators on nesting seabirds in the northeast Pacific. In: Vermeer, K., Briggs, K.T., Morgan, K.H. & Siegel-Causey, D. (Eds.). The status, ecology, and conservation of marine birds of the North Pacific. Ottawa: Canadian Wildlife Service. pp. 218-226.

BENT, A.C. 1919. Notes on birds observed during a brief visit to the Aleutian Islands and Bering Sea in 1911. Smithsonian Miscellaneous Collections. Volume 56, No. 32. Washington: Smithsonian Institution.

BLACK, L.T. 1984. Atka – an ethnohistory of the western Aleutians. Kingston: Limestone Press.

BUSKIRK, S.W. & GIPSON, P.S. 1980. Zoogeography of Arctic Foxes (*Alopex lagopex*) on the Aleutian Islands. In: Chapman, J.A & Pursley, D. (Eds.). Worldwide Furbearer Conference Proceedings, Volume 1. Frostberg: Worldwide Furbearer Conference, Incorporated. pp. 38-54.

BYRD, G.V. & GIBSON, D.D. 1980. Distribution and population status of Whiskered Auklet in the Aleutian Islands, Alaska. *Western Birds* 11:135-140

BYRD, G.V. & WILLIAMS, J.C. 1993. Whiskered Auklet (*Aethia pygmaea*). In: Poole, A. & Gill, F. (Eds.). The Birds of North America, No. 76. Washington: The American Ornithologists' Union.

BYRD, G.V., TRAPP, J.L. & ZEILLEMAKER, C.F. 1994. Removal of introduced foxes: a case study in restoration of native birds. In: Mc Cabe, R.E. & Wadsworth, K.G. (Eds.). Transactions of the 59th North American Wildlife and Natural Resources Conference. Washington: Wildlife Management Institute. pp. 317-321.

BYRD, G.V., BAILEY, E.P. & STAHL, W. 1997. Restoration of island populations of Black Oystercatchers and Pigeon Guillemots by removing Arctic Foxes. *Colonial Waterbirds* 20: 253-260.

CARNARHAN, J. 1979. Fox farming in the Aleutians. In: Spencer, D. (Ed). Aleutian Islands National Wildlife Refuge. Anchorage: U.S. Fish and Wildlife Service. pp. 76-96.

DALL, W.H. 1873. Notes on the avifauna of the Aleutian Islands, especially those west of Unalashka. *Proceeding of the California Academy of Sciences* 5: 270-281.

DAY, R.H. & BYRD, G.V. 1989. Food habits of the Whiskered Auklet at Buldir Island, Alaska. *Condor* 91: 65-72.

EBBERT, S. 2000. Successful eradication of introduced Arctic Foxes from large Aleutian Islands. In: Salmon, T.P. & Crabb, A.C. (Eds.). Proceedings of the 19th Vertebrate Pest Conference. Davis: University of California. pp. 127-132.

EBBERT, S.E. & BYRD, G.V. 2002. Eradications of invasive species to restore natural biological diversity on Alaska

Maritime National Wildlife Refuge. In: Turning the tide: the eradication of invasive species. IUCN SSC Invasive Species Specialist Group. Cambridge: International Union for the Conservation of Nature. pp. 102-109.

GABRIELSON, I.N. 1959. Birds of Alaska. Harrisburg: Stackpole Books.

GASTON, A.J. & JONES, I.L. 1998. The Auks *Alcidae*. Oxford: Oxford University Press.

GRAY, D. 1939. Report on Aleutian Islands. Unpublished U.S. Fish and Wildlife Service Administrative Report.

HUNTER, F.M. & JONES, I.L. 1999. The frequency and function of aquatic courtship and copulation in Least, Crested, Whiskered, and Parakeet auklets. *Condor* 101: 518-528.

HUNTER, F.M., JONES, I.L., WILLIAMS, J.C. & BYRD, G.V. 2002. Breeding biology of the Whiskered Auklet (Aethia pygmaea) at Buldir Island, Alaska. *Auk* 119: 1036-1051.

JONES, R.D. Jr. & BYRD, G.V. 1979. Interrelations between seabirds and introduced animals. In: Bartonek, J.C. & Nettleship, D.N. (Eds.). Conservation of marine birds of northern North America. Wildlife Research Report 11: Washington: U.S. Fish and Wildlife Service. pp. 221-226.

KNUDTSON, E.P. & BYRD, G.V. 1982. Breeding biology of Crested, Least and Whiskered auklets on Buldir Island, Alaska. *Condor* 84: 197-202.

KONYUKHOV, N.B. & ZUBAKIN, V.A. 1994. Paradoxes of the Whiskered Auklet (Aethia pygmaea) II. Return of juveniles to a colony. *Beringian Seabird Bulletin* 2: 60-63.

KONYUKHOV, N.B. 2001. Molting and seasonal bill-plate shedding in the Whiskered Auklet (Aethia pygmaea). *Biological Bulletin of the Russian Academy of Sciences* 28: 266-277.

MURIE, O.J. 1936. Biological investigations – Aleutian Islands and southwestern Alaska April 23-September 19, 1936. Unpublished U.S. Fish and Wildlife Service Administrative Report.

MURIE, O.J. 1937. Supplementary report on the Aleutian Islands, Alaska. Unpublished U.S. Fish and Wildlife Service Administrative Report.

MURIE, O.J. 1959. Fauna of the Aleutian Islands and Alaska Peninsula. *North American Fauna* 61: 1-406.

PITOCCELLI, J., PIATT, J.F. & CARTER, H.R. 2003. Variation in plumage, molt, and morphology of the Whiskered Auklet (*Aethia pygmaea*) in Alaska. *Journal of Field Ornithology* 74: 90-98.

SEKORA, P. 1973. Aleutian Islands National Wildlife Refuge wilderness study. Anchorage: U.S. Fish and Wildlife Service.

SNOW, H.J. 1897. Notes on the Kuril Islands. London: Royal Geographical Society.

STEJNEGER, L. 1885. Results of ornithological explorations in the Commander Islands and in Kamschatka. Bulletin of U.S. National Museum, volume 29 Washington: U.S. Government Printing Office.

TURNER, L.M. 1886. Contributions to the natural history of Alaska. Arctic series of publications in connection with the Signal Service, No. 2. Washington: U.S. Army.

ZUBAKIN, V.A. & KONYUKHOV, N.B. 1999. Biology of reproduction of the Whiskered Auklet (*Aethia pygmaea*): Pattern of nesting, activity, in the colony, and social behavior. *Biological Bulletin of the Russian Academy of Sciences* 26: 460-468.

ZUBAKIN, V.A. & KONYUKHOV, N.B. 2001. Breeding biology of the Whiskered Auklet (*Aethia pygmaea*); Postnesting period. *Biological Bulletin of the Russian Academy of Sciences* 28: 31-39.

ASSESSING CHICK GROWTH FROM A SINGLE VISIT TO A SEABIRD COLONY

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SUMMARY

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We tested an approach to the collection of seabird chick growth data that utilizes a one-time sampling of chick measurements obtained during a single visit to a seabird colony. We assessed the development of Black-legged Kittiwake *Rissa tridactyla* chicks from a sample of measurements made on a single day during six years and compared these results to linear growth rates (g/day), determined from repeated measurements of the same chicks. We used two one-time sampling methods to obtain indices of “chick-condition”, 1) overall body-size (wing, head-plus-bill, tarsus) vs. mass, and 2) wing vs. mass; both were consistent with repeated measurements in identifying annual variations in chick growth. Thus, we suggest that chick-condition indices obtained from measurements collected on a single visit to a seabird colony are a useful tool for monitoring chick growth, especially at colonies where multiple visits and/or repeated measurements of individual chicks are impractical.

Keywords: Alaska, Black-legged Kittiwake, body-condition, chick growth, *Rissa tridactyla*, seabird monitoring

INTRODUCTION

Postnatal development of seabird chicks can be a sensitive indicator of local environmental conditions (Fendley & Brisbin 1977, Ricklefs 1983, Cairns 1987, Montevecchi 1993, Boersma & Parrish 1998). However, collection of detailed growth data, for seabird chicks is often limited by logistics (remote or difficult access to colonies), disturbance to breeding birds, or funding. Depending on the species, it may require 2-4 months of frequent measurements to assess chick growth from hatching to fledging. While studies of chick growth and physiology often demand such detailed measures, investigators often wish to use growth only as an indicator of food abundance during the breeding season. Thus, if we wish to use seabirds as monitors of the marine environment (Cairns 1987, Montevecchi 1993) it will be useful to develop and validate simple methods of assessing chick growth.

Recognizing the inherent difficulty of obtaining growth rates from colonial oceanic species, Ricklefs and White (1975) developed a method to construct an average growth curve for chicks at a seabird colony by collecting wing measurements during two visits to a colony over a 10-day interval. This approach both reduced the sampling effort needed to construct a growth curve and eliminated the need to carefully monitor chick hatch dates and ages. However, it required a second visit to the colony and the ability to recapture and measure previously banded chicks, which would be extremely difficult with species that are loosely nidicolous or form crèches.

A few prior investigators have used single measures from chicks of unknown age to obtain an index of chick growth (Hamer *et al*. 1991, Phillips *et al*. 1996, Suddaby & Ratcliffe 1997). In each of these studies, chick wing-length was used to estimate age, so that age-mass relationships could be evaluated. However, while individual chicks may have been measured only once in these studies, measurements were collected during multiple visits over an entire chick-rearing season, and these results have never been corroborated by comparison with repeated measurements from the same chicks. Furthermore, Øyan and Anker-Nilssen (1996) reported preferential growth of the head in times of food stress for Atlantic Puffin chicks, suggesting that wing length alone may be a poor substitute for chick age.

The simplest method of assessing chick growth would be one that allowed researchers to measure chicks of unknown age while visiting a colony only once per year. For example, to estimate chick growth with minimal disturbance, Uttley *et al*. (1994) measured wing-length and mass of Common Murre *Uria aalge* chicks during a single visit. However, for reasons of differential growth allocation noted above, wing length alone may not always be an accurate estimator of age on which to regress body mass. Therefore, we borrowed a technique often used by studies to compare the body-condition of full-grown animals where multiple body measures are taken and principal components analysis (PCA) is used to calculate a body-size index, which is then regressed with mass (Hamer *et al*. 1993, Jakob *et al*. 1996, Golet *et al*. 1998). We tested these methods on chicks for which there also was a full complement of growth data. We used detailed growth data collected at one colony over a 6 yr period to compare two different single sample methods to one method that incorporates repeated measurements of individual chicks. Our goal was to determine whether chick measures obtained during a single visit to a seabird colony could provide a reliable “chick-condition index”. If valid, this approach could be useful to a wide array of seabird biologists.

METHODS

We measured and weighed chicks at a Black-legged Kittiwake *Rissa tridactyla* colony in Shoup Bay, Prince William Sound, Alaska in 1990, 1995-1999. We checked nests daily to determine hatch dates. We measured chicks every four days from hatching to near-fledging (30 days). Recorded measurements included right tarsus (± 0.1 mm), head-plus-bill (± 0.1 mm), right wing (± 1 mm; from wrist to tip of the longest primary, flattened and straightened), and body-mass (± 1 g). We banded chicks with United States Fish and Wildlife Service stainless steel bands for identification.

To simulate a one-time visit to the breeding colony we used a sub-sample of chick measurements that were obtained on a single day each year between 24 July and 27 July. We then calculated body-size vs. mass relationships for each year using both a single wing measure and principal component scores of multiple body measures. We conducted the PCA on standardized wing, head-plus-bill, and tarsus (measurements were standardized to means of zero and standard deviations of one; Manly 1994). We regressed body-mass on both wing and PCA scores and used the residuals, expressed as a percentage of predicted body-mass, to obtain the chick-condition indices, to be compared among individuals and/or treatment groups. To test the effectiveness of this method with respect to age, we also calculated chick-condition indices (based on PCA scores only) for both younger and older groups of chicks using sub-samples of chick measures occurring approximately 10 days before and after the 24 July and 27 July period.

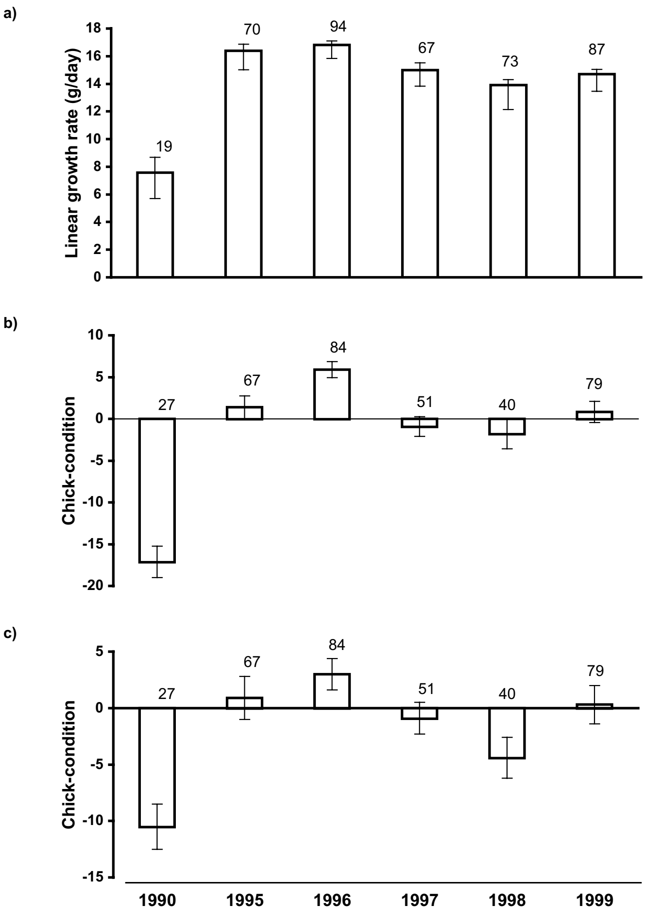

Fig. 1. Linear growth rates as measured over the near-linear 60 to 300 g mass range (a) and chick-condition indices based on overall body-size (b) and wing only (c), both of which used single measures obtained between July 24–27 at the Shoup Bay colony, Prince William Sound, Alaska. Results are presented as means (± standard error) with sample sizes indicated above.

As a basis for comparison, we regressed body-mass on age to calculate growth rates (g/day) of individual chicks within the mass range of 60 to 300 g (Coulson & Porter 1985). The 60 to 300 g growth phase is a sufficiently narrow range to include the near-linear portion of kittiwake growth, except during years when growth is extremely poor; in these cases, some additional points outside the near-linear phase (beyond the asymptotic mass) may be included (Suryan *et al*. 1999).

For comparisons among annual means we used a single factor analysis of variance and Tukey multiple comparison test. We did not use analysis of covariance because it assumes homogeneous slopes and because there is no evidence that hatching weights of kittiwakes differ among years or colony. We conducted all analyses using SAS software. Results were considered significant at $\alpha = 0.05$.

RESULTS

One-time sample methods proved successful in detecting the differences observed in chick growth among years; annual trends in both chick-condition indices were similar to those in linear growth rates (Fig. 1). There was a significant difference among years for linear growth rate ($F_{5,404} = 24.8$, $P < 0.0001$; Fig. 1a). Multiple comparisons revealed that growth rates in 1990 were significantly lower than other years, while growth rates in 1996 were greater than other years, statistically significant in all years except 1995. Additionally, growth rate in 1995 was significantly greater than in 1998 and 1999.

Measures of chick-condition using the PCA based body-size scores were significantly different among years ($F_{5,341} = 21.4$, $P < 0.0001$;

TABLE 1

A comparison of chick-condition for Black-legged Kittiwake chicks measured during 6 yr at the Shoup Bay colony, Prince William Sound, during three periods: July 24-27 (middle period), 10 d earlier (early) and 10 d later (late). The residuals are from linear regression relationships between principal component scores for chicks measured during middle vs. early ($R^2 = 0.60$, $F_{4,5} = 5.84$, $P = 0.073$) and middle vs. late ($R^2 = 0.81$, $F_{4,5} = 17.18$, $P = 0.014$).

	Chick-condition			Residuals	
Year	Early	Middle	Late	Middle vs. Early	Middle vs. Late
1990	-8.77	-17.1	-12.21	-0.01	-0.07
1995	1.95	1.39	3.03	1.27	1.95
1996	3.26	5.9	4.33	0.28	0.02
1997	4.88	-0.93	3.18	5.38	3.76
1998	-3.71	-1.79	-2.76	-2.77	-1.57
1999	-3.76	0.83	-3.4	-4.15	-4.08

Fig. 1b), and multiple comparisons revealed results nearly identical to those of linear growth rate analysis; this method was not able to identify chick-condition in 1995 as significantly greater than in 1998 and 1999.

Measures of chick-condition using wing alone revealed similar trends to both the PCA based index and linear growth rates, however this technique was less sensitive in identifying statistically significant differences in chick development among years (Fig 1c); there was a significant difference among years overall ($F_{5,342} = 5.07$, $P < 0.0002$), but multiple comparison tests were unable to show that chick-condition in 1999 was significantly less than in 1995 and 1996, nor that 1990 was a year of substantially slower growth than 1998.

The initial sub-sampling of one-time chick measures on 24 July and 27 July (roughly middle chick-rearing period) included chicks with a mean age of 20 d (± 5.3 SD, range = 1-33 d, for those chicks of known age) and mass of 308 g (± 78.4, range = 30-463 g). The additional testing of chicks 10 d younger and 10 d older produced results that were mostly similar to the first PCA chick-condition index (R^2 = 0.60 and 0.81 for middle vs. early and late, respectively). These relationships would have been even more similar if it were not for the relatively large residuals for 1997 and 1999 (Table 1). These were the only two years in which chick-condition, relative to the other four years, changed between early, middle, and late chick-rearing (Table 1).

DISCUSSION

Our results suggest that measurements obtained during a single visit to a seabird colony can be used to detect variation in chick growth among years. Given the two methods that we tested, we demonstrated that collecting wing, head-plus-bill, tarsus, and body mass measures to calculate an overall body-size was preferable to collecting only wing and body mass. However, if time or personnel are extremely limited (especially regarding colony or chick disturbance), measuring only wing and body mass is an adequate approach to evaluating chick development during a single visit to the colony.

We selected days from mid-July to simulate a single visit to each colony for two reasons. First, for kittiwakes in the northern Gulf of Alaska, this is typically a period of maximum growth rate (Suryan *et al*. 2002) leading to peak energetic demand for kittiwake chicks (Gabrielsen *et al*. 1992). Therefore, variation in chick development should most likely be expressed at this time. Second, we wanted to use simple linear regression to analyze residual body mass, therefore we restricted our selection of data to the linear growth phase.

However, it is possible employ the one-sample technique at various stages of chick-rearing depending on the question of interest. We demonstrated that the one-sample technique is useful in detecting inconsistent growth patterns within a given year. Indeed, the inconsistent chick-condition indices that we found between early, middle, and late chick-rearing for 1997 and 1999 were also observed with growth trends where, based on logistic curves, in 1997 there was slow initial growth (delayed inflection point) followed by recovery to a high asymptotic mass and in 1999 there was average initial growth (average inflection point) but subsequently reduced growth and lower asymptotic mass (Suryan *et al*. 2002). Such inconsistent, within-year growth patterns were not observed in our chick-condition indices or the logistic growth curves for 1996 (consistently high) or 1998 (consistently low).

Ideally, if chicks are measured only once, they should be measured late in the phase of linear growth so that the index provides an integrated measure of chick growth throughout the chick-rearing period. However, measurements of chicks should be made prior to pre-fledging weight recession (common among seabirds; Ricklefs 1968a,b) because body mass would decline while body size continued to increase, creating misleading results. We also do not recommend applying this method to very young chicks because they are relatively homogeneous in body size and mass in early development. Therefore, this method should work best for a species with a relatively predictable breeding schedule so that a visit to the colony can be made during the appropriate sampling window. Conversely, its usefulness may be limited for species' whose timing of breeding varies a lot. Additional consideration should be given to species that have multi-chick broods; if possible, chick order should be distinguished and analyzed separately.

This snapshot approach to assessing variation in chick growth is not recommended as a substitute for measuring complete growth curves. Variations in food supply or environment at different stages of chick rearing can alter the growth rate, duration of growth, and asymptotic mass of chicks so that birds growing at a slower rate may complete growth at a higher mass and vice-versa (Ricklefs 1968a, Suryan *et al*. 2002). For some birds, e.g. the Alcidae (Gaston 1985, Øyan and Anker-Nilssen 1996) growth in all linear dimensions may be retarded when rate of mass gain is slow, so this method may not be able to discriminate between a year of late hatching and a year of slow growth. This flexibility warrants caution when interpreting results. On the other hand, for kittiwakes in this study, it appeared that growth of the organs measured was fairly determinate and that mass was affected more than body parts, thus we recommend this approach for kittiwakes and believe that it should be a useful tool for monitoring other species at colonies subject to brief visits. Such a chick-condition index should provide a useful indication of chick growth and development, and indirectly allow inference about abundance of food supplies during the breeding season.

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REFERENCES

BOERSMA, P.D. & PARRISH, J.K. 1998. Flexible growth in fork-tailed storm-petrels: a response to environmental variability. *Auk* 115: 67-75.

CAIRNS, D.K. 1987. Seabirds as indicators of marine food supplies. *Biological Oceanography* 5: 261-267.

COULSON, J.C. & PORTER, J.M. 1985. Reproductive success of the kittiwake *Rissa tridactyla*: the roles of clutch size, chick growth rates and parental quality. *Ibis* 127: 450-466.

FENDLEY, T.T. & BRISBIN, I.L., Jr. 1977. Growth curve analyses, a potential measure of the effects of environmental stress upon wildlife populations. *International Congress of Game Biologists* 13: 337-350.

GABRIELSEN, G.W., KLASSEN, M., & MEHLUM, F. 1992. Energetics of black-legged kittiwake *Rissa tridactyla* chicks. *Ardea* 80: 29-40.

GASTON, A. J. 1985. Development of the young in the Atlantic Alcidae. In: Nettleship, D.N. & Birkhead, T.R. (Eds.). The Atlantic Alcidae. Academic Press, London: pp. 319-354.

GOLET, G.H., IRONS, D.B. & ESTES, J.A. 1998. Survival costs of chick-rearing in black-legged kittiwakes. *Journal of Animal Ecology* 67: 827-841.

HAMER, K.C., FURNESS, R.W. & CALDOW, R.W.G. 1991. The effects of changes in food availability on the breeding ecology of Great Skuas *Catharacta skua* in Shetland. *Journal of Zoology, London* 223: 175-188.

HAMER, K.C., MONAGHAN, P., UTLEY, J.D., WALTON, P. & BURNS, M.D. 1993. The influence of food supply on the breeding ecology of kittiwakes *Rissa tridactyla* in Shetland. *Ibis* 135: 255-263.

JAKOB, E. M., MARSHALL, S.D. & UETZ, G.W. 1996. Estimating fitness: a comparison of body-condition indices. *Oikos* 77: 61-67.

MANLY, B. F. J. 1994. Multivariate statistical methods: a primer. 2nd ed. London: Chapman & Hall. Chap. 6, Principal components analysis; pp. 76-92.

MONTEVECCHI, W.A. 1993. Birds as indicators of change in marine prey stocks,. In: . Furness, R.W. & Greenwood, J.J.D. (Eds.). Birds as monitors of environmental change. Chapman and Hall, London: pp. 217-266.

ØYAN, H.S. & ANKER-NILSSEN, T. 1996. Allocation of growth in food-stressed Atlantic Puffin chicks. *Auk* 113: 830-841.

PHILLIPS, R. A., CALDOW, R.W.G. & FURNESS, R.W. 1996. The influence of food availability on the breeding effort and reproductive success of Arctic Skuas *Stercorarius parasiticus*. *Ibis* 138: 410-419.

RICKLEFS, R.E. 1968a. Patterns of growth in birds. *Ibis* 110: 419-451.

RICKLEFS, R.E. 1968b. Weight recession in nestling birds. *Auk* 85: 30-35.

RICKLEFS, R.E. & WHITE, S.C. 1975. A method for constructing nestling growth curves from brief visits to seabird colonies. *Bird-Banding* 46: 135-140.

RICKLEFS, R.E. 1983. Avian postnatal development, p 1-83 In: Avian Biology, Vol.VII. Academic Press, Inc.

SAS. 1989. SAS/STAT user's guide. Version 6. SAS Institute, Cary, North Carolina, USA.

SUDDABY, D. & RATCLIFFE, N. 1997. The effects of fluctuating food availability on breeding Arctic Terns (*Sterna paradisaea*). *Auk* 114: 524-530.

SURYAN, R.M., IRONS, D.B., KAUFMAN, M., BENSON, J., JODICE, P.G.R., ROBY, D.D. & BROWN, E.D. 2002. Short-term fluctuations in forage fish availability and the effect on prey selection and brood-rearing in the Black-legged Kittiwake *Rissa tridactyla*. *Marine Ecology Progress Series* 236: 273-287.

SURYAN, R.M., ROBY, D.D., IRONS, D.B. & PIATT, J.F. 1999. An evaluation of methods for determining growth rates of nestling seabirds. In: Kittiwakes as indicators of forage fish availability. *Exxon Valdez* oil spill restoration project annual report (project 98163E). U.S. Fish and Wildlife Service, Anchorage, Alaska.

UTLEY, J. D., WALTON, P., MONAGHAN, P. & AUSTIN, G. 1994. The effects of food abundance on breeding performance and adult time budgets of Guillemots *Uria aalge*. *Ibis* 136: 205-213.

A REVIEW OF FOUR SUCCESSFUL RECOVERY PROGRAMMES FOR THREATENED SUB-TROPICAL PETRELS

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SUMMARY

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Recovery programmes have significantly increased the population sizes of four threatened sub-tropical petrels: Zino's Petrel *Pterodroma madeira*, Bermuda Petrel *P. cahow*, Gould's Petrel *P. leucoptera* leucoptera and Hawaiian Petrel *P. sandwichensis*. These recovery programmes were reviewed to examine i) past and present nesting habitat; ii) the nature and commonality of threats; iii) the recovery actions undertaken; iv) the conservation gains; and v) the factors most responsible for these gains. The most significant causes of past population decline were exploitation by humans for food, loss of nesting habitat and the introduction of alien mammals. Primary contemporary threats are predation and disturbance at the breeding grounds by both alien and indigenous species. Current relict populations have restricted distributions and are often confined to nesting habitats that are severely degraded or sub-optimal and dissimilar from those known historically. The crucial attribute of these habitats is the absence or low density of alien predators. The most beneficial recovery actions involved the control or eradication of predators at breeding grounds and the provision of safe artificial nest sites. Recovery actions were more difficult to implement for species on large islands. The success of each recovery programme was due largely to concerted action spanning several decades.

Keywords: Zino's Petrel, *Pterodroma madeira*, Bermuda Petrel, *Pterodroma cahow*, Gould's Petrel, *Pterodroma leucoptera*, Hawaiian Petrel, *Pterodroma sandwichensis*, conservation, Procellariiformes

INTRODUCTION

Many petrels (Procellariiformes) have undergone substantial declines in recent times (Harris 1970, Warham 1990). Conservation efforts to curb this trend that have attracted most publicity are those aimed at decreasing the accidental mortality of seabirds in fishing operations, particularly longlining (Baker *et al*. 2002). This particular threat, however, generally affects only the largest and most charismatic species - the albatrosses, giant petrels and a few of the larger shearwaters (Brothers *et al*. 1999). These species are particularly vulnerable to longlining because of their habit of congregating around ships (Ryan & Moloney 1988) to feed on discarded offal and fish bycatch (Croxall & Prince 1994). Smaller petrels (those less than 600 g) tend not to follow ships and so are generally not at risk from longline fishing (Baker *et al*. 2002).

Many small petrels have suffered substantial declines, due primarily to threats at their breeding grounds (Warham 1990). Unlike the majority of larger petrels that nest on sub-Antarctic islands, many smaller species nest in the tropics or sub-tropics, where the threats are often exacerbated by human population pressures (Enticott & Tipling 1997). Tropical and sub-tropical petrels now constitute a significant proportion of threatened Procellariiformes, particularly among those weighing less than 600 g. The most significant threats for petrels breeding in warmer climes include habitat degradation and predation by alien mammals, loss of habitat through agricultural clearance and urbanisation, and harvesting of eggs or young for food (BirdLife International 2000). Many sub-tropical petrels are known only from single islands, and consequently are particularly susceptible to extinction. At least three species are so rare that their current breeding grounds are unknown: Beck's Petrel *Pseudobulweria becki*, Fiji Petrel *P. macgillivrayi* and Jamaica Petrel *Pterodroma caribbaea*.

Despite the global decline of many tropical and sub-tropical petrels several case histories demonstrate that recovery of such species is possible. This paper reviews the recovery programmes of four sub-tropical petrels: Zino's Petrel *Pterodroma madeira*, Bermuda Petrel *P. cahow*, Gould's Petrel *P. leucoptera leucoptera* and Hawaiian Petrel *P. sandwichensis*. The review aims to i) compare past and present nesting habitat; ii) examine the nature and commonality of threats affecting these petrels; iii) scrutinise the recovery actions that have been implemented; and iv) examine the conservation gains that have been achieved. We then explore the various aspects of these recovery programmes to assess whether there were any specific features that were particularly instrumental in the success of these programmes.

TABLE 1
Attributes of the four species of *Pterodroma* petrels reviewed

	Zino's Petrel	Bermuda Petrel	Gould's Petrel	Hawaiian Petrel
Conservation status	Critically endangered	Endangered	Vulnerable	Vulnerable
Known residual population (breeding pairs) and year	7 (1969)	18 (1960)	< 250 (1992)	Unknown (1953)
Known current population (breeding pairs)[a]	29	56	911	c. 1000 on Maui; possibly many thousands on other islands
Former breeding distribution	Widespread on Madeira and on the nearby island of Porto Santo	Widespread across the islands of Bermuda	Restricted to Cabbage Tree and Boondelbah Islands, Australia	Abundant on all large islands in the Hawaiian Islands, USA
Location of contemporary nesting grounds	Steep inaccessible ledges in the Central Mountain Massif of Madeira, Portugal	Islets off Nonsuch Island, Bermuda	Areas of rock scree on Cabbage Tree and Boondelbah Islands, Australia	At high elevations on Maui, Hawaii and probably Kauai and Lanai, Hawaiian Islands, USA.
Size of island(s) containing nesting ground(s)	736 km^2	< 0.01 km^2	Cabbage Tree Island, 0.30 km^2; Boondelbah Island, 0.12 km^2	Maui, 1903 km^2; Hawaii, 10 434 km^2; Kauai, 1435 km^2, Lanai 358 km^2
Original nesting habitat	Unknown. Presumed to nest in soil burrows at a range of altitudes in forest and more open country	Soil burrows in forest	Rock cavities among rock-scree slopes in sub-tropical rainforest	Soil burrows in forests and more open country at lower elevations
Current nesting habitat	Soil burrows on isolated steep ledges, high in the central mountains	Rock cavities on rocky islets with sparse vegetative cover	Rock cavities among exposed rock-scree slopes in sub-tropical rainforest with degraded understorey, and nest boxes	Cavities in volcanic debris in sparsely vegetated, volcanic landscapes generally above 2500 m. Possibly also altitudinal wet forest.
Reasons for population decline	Harvested by humans. Predation by rats and cats. Degradation of nesting habitat by sheep and goats	Harvested by humans. Predation by pigs, cats, dogs and rats. Loss of nesting habitat through urbanisation and farming	Habitat degradation by rabbits. Predation by currawongs and raptors. Entanglement in sticky fruits of *Pisonia umbellifera*	Harvested by early Hawaiians. Loss of nesting habitat due to urbanisation and degradation by feral goats and pigs. Predation by introduced mongoose, feral cats, rats and dogs
Current threats	Predation by rats and cats; habitat loss from sheep and goats; ecotourism	Nest-site competition; predation by rats and raptors; storm surge and storm damage to habitat	Predation by currawongs	Predation by rats, cats, mongoose and dogs; habitat disturbance by goats, pigs and cattle; grounding of fledglings by artificial lights
Methods of predator control	Rats poisoned, cats trapped	Rats poisoned, raptors shot	Currawongs shot	Rats poisoned, cats and mongoose trapped, dogs excluded
Recovery actions	Monitor breeding; trap cats; poison rats; search for new nesting ledges; control ecotourism; education	Monitor breeding; exclude competing species; provide artificial nest sites; control rats	Monitor breeding; control currawongs; prevent regeneration of *Pisonia umbellifera* within nesting grounds; translocation	Monitor breeding; exclude goats, pigs, cattle and dogs; control rats, cats and mongoose; retrieval of grounded birds; search for additional breeding grounds

[a] Data as at the 2000 or 2000-01 breeding season

STATUS AND BREEDING BIOLOGY

All four species reviewed differ in population size, distribution and extent of breeding grounds, nesting habitat and conservation status (Table 1). Based on the then criteria of the World Conservation Union (IUCN 1994), Zino's Petrel (ZP) is Critically Endangered, Bermuda Petrel (BP) is Endangered and both Gould's Petrel (GP) and Hawaiian Petrel (HP) are Vulnerable (BirdLife International 2000).

The four species have similar breeding biology. Like most other Procellariiformes, they are highly pelagic, long-lived, mate for life, breed once a year (some other species breed biennially), and lay a single egg that is not replaced if lost (Warham 1990). Nest-site fidelity is strong, with pairs returning to the same burrow year after year. They feed principally on fish, squid and crustaceans at foraging areas that are largely unknown (Warham 1990).

HISTORIC DISTRIBUTION, HABITAT AND CAUSES OF DECLINE

Zino's Petrel

ZP occurs only on the heavily populated north Atlantic island of Madeira (32° 45' E, 16° 28' N) off the coast of North Africa, 900 km from Portugal, to which the island belongs. Since the island was discovered in 1419, humans have heavily exploited its abundant avifauna as a source of food (Bannerman & Bannerman 1965). The first specimens of ZP were collected in 1903 (Schmitz 1905). By 1934, when the species was first described (Mathews 1934a), it was already rare (Mathews 1934b). In the early 1940s two freshly fledged juveniles were found within the walls of the governor's palace in Funchal, presumably attracted there by lights. The species was not seen again until 1969.

Fossil records indicate that ZP was once widespread and common on Madeira (Zino & Zino 1986) and on the nearby island of Porto Santo (Zino *et al*. 2001). The main island of Madeira (736 km^2) is principally volcanic in origin with precipitous sea cliffs, a central mountain massif (rising to 1860 m) and steep gorges (Maul 1965). The island was once much more forested than it is today (Bannerman & Bannerman 1965) and it is thought that ZP had then nested in a broader range of habitats.

Initially, ZP was almost certainly exploited as a source of food, but would have also been adversely affected by predation from introduced Black Rats *Rattus rattus* and domestic cats *Felis catus*. Its nesting habitat has been eroded through overgrazing, and its burrows have been trampled by domestic stock (sheep *Ovis aries* and goats *Capra hircus*). ZP are now restricted to small cliff ledges that are inaccessible to large mammals.

Bermuda Petrel

BP has only ever been recorded from the Atlantic islands of Bermuda (64º 45' W, 32º 17' N), isolated in the western reaches of the Sargasso Sea, 1200 km north-east of the Caribbean and 900 km east of the United States coastal area of North Carolina (BirdLife International 2000). Bermuda consists of one main island and numerous smaller nearby islands - a total land area of only 53 km^2, supporting a human population of 60 000. The terrain is predominantly hilly, and soils are derived from calcareous sediments of aeolionite (Land & Mackenzie 1970).

Fossil evidence indicates that BP was once common and widespread across much of the main island, as well as on many of the smaller, vegetated islands (Wetmore 1962) where it bred in burrows dug into the soil. BP was first reduced in numbers by domestic pigs Sus scrofa released by Spanish voyagers about 1560 (Wingate 1985). Colonisation of Bermuda by the British in 1612 led to a further decline of the species. Not only was BP exploited as a food source by the early settlers, it was also subjected to heavy predation from introduced domestic cats, domestic dogs Canis domesticus and Black Rats (Lefroy 1877). The species was all but extirpated by around 1630 (Zimmerman 1975) and for more than 300 years was thought to be extinct (Verrill 1902, Murphy & Mowbray 1951).

Gould's Petrel

GP breeds only on two islands - Cabbage Tree Island (152º 14' E, 32º 41' S) and Boondelbah Island (152º 14' E, 32º 42' S) at the entrance to Port Stephens on the east coast of New South Wales, Australia (Priddel & Carlile 1997a). Cabbage Tree Island (0.3 km^2), the principal nesting site, is dominated by sub-tropical rainforest growing on volcanic-derived soils of toscanite. GP nests in natural rock cavities within the forested rock scree slopes of two large gullies on the western side of the island (Hindwood & Serventy 1943). Soil suitable for burrowing is available, but GP does not nest in soil burrows. A few pairs also breed on nearby Boondelbah Island where there is no forest or canopy cover. Here the petrels nest in small, exposed rock piles (Priddel & Carlile 1997a).

GP was first described in 1844 as breeding on Cabbage Tree Island "in great numbers" (Gould 1844), but one hundred years later the population was noticeably less numerous (D'Ombrain 1943). Underlying this decline has been the long-term degradation of the nesting habitat by the introduced European Rabbit *Oryctolagus cuniculus* (Priddel *et al*. 2000). By removing the rainforest understorey, rabbits have removed the vegetative cover that concealed and protected the petrels from avian predators. Removal of the undergrowth also exposed GP to another threat – entanglement in the fruits of the Birdlime Tree *Pisonia umbellifera* (D'Ombrain 1970, Fullagar 1976). This tall, indigenous shrub produces sticky fruits that readily adhere to the feathers of birds, rendering flight impossible (Priddel & Carlile 1995b). In a forest without rabbits, most of the fallen fruits lodge in the understorey plants where they pose little threat to GP. With the understorey removed, the *Pisonia* fruits fall to the ground where they are a significant threat to GP moving about the forest floor.

Hawaiian Petrel

HP breeds only on the Hawaiian Islands in the central Pacific Ocean (Richardson & Woodside 1954). This archipelago is made-up of eight large islands (between 154° W 19° N, and 160° W, 22° N) and 124 smaller islands (between 180° W and 30° N) (Juvik & Juvik 1998). The islands are all volcanic in origin, the most easterly of which are still active. Fossil evidence indicates that HP occurred on numerous islands within the archipelago (Olson & James 1982a, Olson & James 1982b), nesting in soil burrows within altitudinal wet forest (Bryan 1908). Breeding colonies, however, no longer occur on many islands.

The arrival of Polynesians at the Hawaiian Islands some 1800 years ago introduced humans as a major predator of HP. Along with humans came dogs, pigs and the Pacific Rat *R. exulans* (Simons

1985). HP on Oahu was probably exterminated by these alien predators prior to the arrival of Europeans (Olson & James 1982a). Additional mammalian predators that accompanied Europeans, such as domestic cats, Black Rats and Norway Rats *R. norvegicus*, accelerated the declime of HP. The introduction of the Small Indian Mongoose *Herpestes auropunctatus* by the sugar industry added yet another predator (Hodges 1994).

CONTEMPORARY DISTRIBUTION, HABITAT AND THREATS

Zino's Petrel

It was not until 1967 that concerted efforts were made to locate the breeding grounds of ZP (Zino & Zino 1986). In 1969, a relict population was discovered nesting on a series of remote cliff ledges in the Central Mountain Massif (Zino & Zino 1986). These ledges are inaccessible to sheep and goats, and so support floral communities that differ from those on surrounding lands (Zino *et al*. 2001).

Contemporary threats to ZP were initially thought to involve the incidental consumption of birds and eggs by local shepherds and the occasional removal by collectors (Zino & Zino 1986). However, when nests were first monitored (in the early 1980s) it soon became apparent that high levels of predation on eggs and chicks by Black Rats was the predominant threat to the species (Zino & Zino 1986). A further threat was identified in 1991 when feral cats killed 10 petrels on a single ledge (Zino 1992).

Bermuda Petrel

Following many failed attempts to locate living specimens, BP was eventually discovered breeding on several small islets off Nonsuch Island in 1951 (Murphy & Mowbray 1951). It was not until 10 years later, however, that the size of the relict population, just 18 breeding pairs, became known (Zimmerman 1975). The petrels were restricted to four small rocky islets totalling less than 0.01 km^2. These islets are essentially devoid of vegetative cover (Wingate 1988) and contain only small pockets of skeletal soil (Murphy & Mowbray 1951) that are too shallow to support burrows. Without the opportunity to burrow, BP nests in natural rock cavities (Wingate 1985). Many of these cavities are close to sea level and are subject to inundation by surging seas during storms. In addition, hurricanes and rising sea levels are gradually destroying these cavities, reducing further the few nest sites available (Wingate 1995).

The loss of nest sites is compounded by the associated increase in competition from the White-tailed Tropicbird *Phaethon lepturus* (Wingate 1985). This tropicbird, which remains common on Bermuda, is larger and more aggressive than BP and consequently competition for nest sites invariably results in the petrel chick being killed. In some years, mortality of BP chicks has been as high as 60% (Wingate 1985).

Even on the islets where BP currently survives, eggs and chicks were probably lost occasionally to Black and Norway Rats, before measures were taken to control those individuals that manage to reach the islets (Wingate 1978). Occasional predation by owls and falcons (D.B. Wingate unpubl. data) has reduced the rate of recovery of BP.

Gould's Petrel

Monitoring of GP began in 1989. It was soon apparent that the population was declining due to poor breeding success and high adult mortality (Priddel & Carlile 1995b). In 1992, the breeding population numbered less than 250 breeding pairs. Breeding success was poor (<20%) and adult mortality (>50 individuals a year) exceeded fledgling production.

Degradation of the nesting habitat by rabbits had made GP vulnerable to entanglement in the sticky fruits of the Birdlime Tree, and to attack by Pied Currawongs *Strepera graculinaa*, a large, indigenous crow-like bird (Priddel & Carlile 1995b). In addition, sporadic predation by transient raptors and owls occasionally caused significant mortality of breeding adults.

Hawaiian Petrel

Contemporary breeding grounds of the HP were unknown until 1953 when a population was discovered on Maui (Richardson & Woodside 1954). Since then, additional populations have been located on the same island (Harrison *et al*. 1984, Simons 1985, Simons & Hodges 1998, Hodges & Nagata 2001), and on the island of Hawaii (Hu 1995). Haleakala National Park, on the island of Maui, contains the largest known colony of about 1000 breeding pairs (Haleakala National Park unpubl. data). Early reports of Polynesian hunting parties having to travel to the crater of Haleakala to collect fledglings (Henshaw 1902) suggest that HP was already restricted to its current breeding range at the time Europeans arrived in the Hawaiian Islands.

Monitoring of known nests at Haleakala has been conducted annually since 1988, and additional nests are found each year (Hodges & Nagata 2001). In some years more than 60% of all egg and chick mortality was caused by cats and mongooses (Simons 1983). Although rats prey on HP eggs, the major threat that rats pose is that they provide a prey base for cats and mongooses (Simons 1985).

The few sites where HP are currently known to breed are in sub-humid, sub-alpine, volcanic landscapes at altitudes generally above 2500 m (Simons & Hodges 1998). Boulders and debris from volcanic activity dominate this dry, barren landscape where soil and vegetative cover are sparse (Simons 1985). Here HP nests on volcanic cliffs and steep slopes in burrows formed from deep natural cracks between buried rocks, volcanic boulders and bedrock (Richardson & Woodside 1954) or dug into erosional debris or, occasionally, sod-covered soil (Simons 1985).

Based on at-sea observations, Spear *et al*. (1995) estimated the world population of HP to be about 19 000 birds. Nocturnal calls and the occurrence of grounded fledglings suggest that the species may breed on the islands of Kauai and Lanai, but difficult terrain has so far frustrated attempts to locate any colonies (Hirai 1978, Conant 1980, Ainley *et al*. 1997). Based on the number of birds observed returning inland the as-yet-undiscovered population on Kauai may exceed several thousand individuals (Ainley *et al*. 1997) and may still nest in soil burrows within forest (Simons & Hodges 1998). This population may be relatively abundant because Kauai is free of mongooses.

OTHER POTENTIAL THREATS

Pollutants

Of the four petrel species considered in this review, pollution is known to affect only one. BP was discovered to have high levels of residual DDT in chicks and eggs (Wurster & Wingate 1968). This residual insecticide was implicated in the low reproduction success recorded between 1958 and 1970. Although plastic pollution is a significant threat to many seabirds, it does not appear to be a threat for any of the four species of petrel reviewed. Opportunistic examinations of the regurgitated crop contents of ZP, HP and GP found no evidence of synthetic material (Zino *et al*. 1989, C. Natividad & D. Priddel unpubl. data). There are no records of oil contaminating any of the four species.

Threats at sea

The range and extent of threats at sea are essentially unknown for all four species, largely because very little is known about the extent or whereabouts of their foraging areas. Spear *et al*. (1995) conducted at-sea observations of HP and other Procellariiformes between 1980 and 1994. While valuable information was gathered on distribution, density and population size, little was revealed about possible threats.

Although there is no evidence of any current threats at sea for any of the four species, two observations highlight their sensitivity to conditions at sea. Firstly, a dramatic reduction in breeding success of GP (<20% compared to the norm of >50%) occurred during 1995 (Priddel & Carlile 1997b) coincident with an Australia-wide die-off of Pilchards *Sardinops sagax neopilchardus*, believed to be the result of an alien pathogen introduced to Australian waters in frozen pilchards fed to farmed fish (Hyatt *et al*. 1997). Secondly, the percentage of HP that come ashore to nest is significantly less during *El Niño* years (c. 40% compared to the norm of c. 65%; C.N. Hodges *in litt*.). These responses suggest that sub-tropical petrels may be particularly vulnerable to an increase in the extent or frequency of environmental perturbations caused by further degradation of the marine environment or by global climate change.

RECOVERY ACTIONS

Actions completed

For each recovery programme, a suite of recovery actions has been implemented to ameliorate each of the threats identified, minimise adult mortality and maximise reproductive output. Although the collective benefit of these actions has been measured, the relative contribution of each individual action has not been assessed.

Although the breeding grounds of ZP were rediscovered in 1969, it was not until 1986 that the Freira Conservation Project was established to protect the species. This programme was a joint initiative between the Funchal Museum of Natural History, Parque Natural da Madeira and the local community, with financial assistance provided by several European benefactor agencies. Responsibility for development, coordination and implementation of the programme has rested with concerned local ornithologists. The programme aimed to monitor the breeding population, ameliorate threatening processes as they were identified and to investigate further possible breeding sites (Zino *et al*. 2001). In 1986 a programme of rat baiting was instigated (Buckle & Zino 1989). Following a bout of cat predation in 1991 an intensive cat-trapping programme was also initiated (Zino 1992).

BP has had the longest programme of recovery, beginning in 1951 and, up until recently, under the stewardship of a single individual. Actions to conserve BP have focused on reducing competition for nest sites, providing artificial nest sites and rat control. Initial recovery action involved fitting each nest site with a wooden baffle that restricted entry by tropicbirds but permitted access by the slightly smaller petrels (Zimmerman 1975). Subsequently, artificial nest sites were also created. These structures, comprising a long tunnel terminating in an enlarged chamber, were constructed largely of concrete (Wingate 1978). Construction of these artificial nests has continued to ensure that there are at least 10 nests surplus to requirements each year. Following each major storm, substantial remedial work is needed to shore up eroding sections of the smaller islets and prevent the loss of nest sites. Rats have been eradicated from the small islets, but occasionally this needs to be repeated because of re-invasion from adjacent headlands of the main island (Wingate 1985). Baiting of these headlands to reduce the likelihood of recolonisation is now a routine part of the recovery programme.

The plight of GP came to light only as recently as 1989 (Priddel *et al*. 1995). In 1993, concerned scientists initiated an experimental recovery programme to remove Birdlime Trees from within the GP breeding habitat and to control Pied Currawongs (Priddel & Carlile 1997b). In 1997, rabbits were eradicated from Cabbage Tree Island (Priddel *et al*. 2000). Over the next few years, two hundred near-fledged birds were translocated from Cabbage Tree Island to Boondelbah Island, one kilometre to the south, and placed in habitat created from artificial nest boxes (Priddel & Carlile 1995a). The aim was to establish a second colony as a safeguard for the species should the main colony on Cabbage Tree Island suffer catastrophic loss due to wildfire or the arrival of an alien predator. Earlier trials demonstrated the validity of the techniques used (Priddel & Carlile 2001), but it is too soon to know if the translocation has been successful.

In 1976, a perimeter fence was erected around the main colony of HP to exclude feral goats and pigs. Although the purpose of this fence was to protect the endemic vegetation (Hodges 1994), it also benefited HP by preventing burrows from being trampled (Simons 1983). The fence also reduced the number of dogs entering the colony (Hodges & Nagata 2001). Trapping to control rats began in 1968. Since 1981, cats and mongooses have also been targeted following studies which highlighted the impact of these species. Trapping of all three species is now undertaken year-round, with the additional use of rodenticides since 1997. Urban lighting on Kauai has been modified to reduce the number of young HP and Newell's Shearwater *Puffinus auricularis newelli* that become disorientated and ground on the island (Ainley *et al*. 1995, Simons & Hodges 1998).

Proposed actions

ZP is far from secure, and although over time the threat of illegal collecting has diminished, ecotourism from ornithologists and mountaineers is expanding and needs to be appropriately managed (Zino *et al*. 2001). With the assistance of international funding, the land containing the ledges on which ZP breeds are being purchased as a conservation measure. Grazing has already been excluded. Together these actions will control erosion, restore the vegetative cover, and expand the extent of suitable nesting habitat. Initially, the expansion of nesting habitat may involve the creation of artificial burrows. A study of burrow usage by breeding adults, using remote electronic techniques, is soon to commence.

A programme of banding BP has recently been instigated to collect detailed information regarding the demography of this species. Initiatives to attract sub-adults to other islands or to translocate fledglings from some of the smaller islets to Nonsuch Island (0.06 km^2) are currently being developed. Nonsuch is maintained predator free, contains a regenerated forest environment and has excellent potential to allow the petrels to recommence their natural burrowing activities (Wingate 1985).

The recovery of GP is progressing at such a rate that no additional recovery actions are planned (NSW National Parks and Wildlife Service 2001). A study is currently being undertaken to examine the energetics of breeding adults and nestlings. The findings of this study may provide options to maximise reproductive output should food resources again be in short supply.

Further surveys are needed to locate colonies of HP on Kauai and additional colonies on the island of Hawaii. Despite best efforts, the control of predators at Mauna Loa on the island of Hawaii needs to be improved. Current practices of predator control at Haleakala on Maui appear adequate, but research to improve the efficiency of the techniques used is likely to be beneficial (Simons & Hodges 1998).

CONSERVATION ACHIEVEMENTS

In the first year of monitoring (1986) the breeding success of ZP, only six burrows on the main nesting ledge were occupied, and no pairs bred successfully (Zino & Zino 1986). Rat baiting began soon after and in 1987 a single chick survived through to fledging (Buckle & Zino 1989). Since 1990, breeding success has been variable, but the number of known breeding pairs on this ledge has increased to 12 (Zino *et al*. 2001), with a further 17 pairs discovered on other ledges.

Recovery of BP was variable in the early years. Breeding success increased to 66% (18 breeding pairs) in 1960 but dropped to a low of 28% in 1966 (21 pairs) (Wurster & Wingate 1968). By 1977, the number of breeding pairs had risen to 26 and breeding success had stabilised at approximately 50–60% (Wingate 1978). The population has continued to increase steadily, reaching 35 breeding pairs in 1983 (Wingate 1985), 49 in 1995 (Wingate 1995) and 56 in 2000 (D.B. Wingate unpubl. data). The presence in recent years of additional birds prospecting for nest sites suggests that the increasing trend will continue into the foreseeable future.

In 1992, the population of GP was less than 250 breeding pairs, breeding success was less than 20% and fewer than 50 young fledged a year (Priddel *et al*. 1995). Recovery actions have been implemented since 1993, and the number of breeding pairs has increased steadily to 911 pairs breeding in 2000 (D. Priddel & N. Carlile unpubl. data). Breeding success has, in all but one year, exceeded 50%. Reproductive output has increased markedly, and in 2000 a total of 474 birds fledged.

Many nesting grounds of HP remain undiscovered, so the size of the population and the rate of recovery are difficult to estimate. In 2000, the known breeding population was estimated to be 450–650 pairs (Hodges & Nagata 2001). Annual surveys have now located a total of more than 900 HP nests around the summit of Haleakala alone (Hodges & Nagata 2001). Further nests are likely to be discovered as more potential sites are searched. Estimates of population size based on observations of birds at sea (Spear *et al*. 1995) and birds flying inland on Kauai Island (Ainley *et al*. 1995) range up to 35 000 birds. In 1979, breeding success (based on the proportion of active burrows that produce fledglings) at Haleakala was 24%, with most breeding failure being due to predation (Simons 1985). Since recovery actions have been implemented breeding success appears stable at about 40% (Simons 1985, Hodges 1994, Hodges and Nagata 2001).

DISCUSSION

Current populations of all four petrels now have greatly restricted distributions and are confined to habitats that differ markedly from their original nesting habitat (Table 1). By inhabiting uncharacteristic or sub-optimal habitats petrels can be exposed to threats that they would not normally encounter. BP, for example, now breeds on islets where it suffers nest competition with the cliff-nesting tropicbird and inundation of nests by seas during storms. Neither of these problems would have occurred in the original breeding habitat.

Although current nesting habitats bear little resemblance to those used in the past, they share one crucial attribute: the absence or low density of alien predators. Thus, whereas forest may be a component of the optimal nesting habitat for these petrels, the principal factor in conserving each species is maintaining their current nesting habitat free of alien predators. It is not surprising then that the recovery action that featured most prominently in each of the four recovery programmes was the control of predators. The species of predator differed between programmes, so the means of control also varied (Table 1).

Predation of nesting adults, chicks and eggs is probably the single most significant threat to petrel populations around the globe, and is particularly prevalent at tropical and sub-tropical latitudes (Enticott & Tipling 1997, BirdLife International 2000). Troublesome predators can also include indigenous species that have assumed pest status. Both BP and GP have suffered significant losses from indigenous bird species, these threats having arisen in response to the changing circumstances associated with displacement from, or degradation of, optimum habitat.

Each of the recovery programmes focused on enhancing small relict populations of species that were once far more numerous. Relict populations can be particularly difficult to locate, thereby delaying or frustrating efforts to commence recovery action. Three species (ZP, BP, HP) were eventually discovered in habitats dissimilar from those in which they previously occupied when more abundant. Surveys for other populations and other relict species should extend beyond those habitats known from historical records.

All four species of petrel showed substantial increases in breeding success soon after action was taken to ameliorate the threats identified. However, because petrels are long-lived and can take many years to reach breeding age (usually in excess of five years; Warham 1990), increases in the size of the breeding population can be slow, and may not be evident for many years. It is essential, therefore, that recovery programmes for seabirds are planned and funded in terms of decades rather than years. Often financed by short-term political budgets, conservation agencies around the world have difficulty in planning and maintaining such long-term programmes. An important feature of each of the programmes reviewed is their relative longevity, due in large part to a few dedicated individuals. It is noteworthy that the successes associated with these recovery programmes have been achieved primarily by individuals who worked to some extent independently of conventional funding and organisations, and without the guidance of a recovery team or any formal review process. Although many nations now have a formal recovery planning process in place, usually involving the formulation of a recovery plan overseen by a recovery team, this procedure is clearly not essential to achieving a successful conservation outcome. Of those species reviewed, BP and GP have the smallest breeding distributions. Being restricted to small, uninhabited islands, however, has meant that recovery actions could be more focused and more effective. The total area requiring management is comparatively small, making tasks such as the control or eradication of alien predators both achievable and affordable. On the other hand, species that nest on large islands generally require management that is both more extensive and more frequent, thus necessitating greater overall effort to achieve the same results. HP and ZP breed on relatively large islands (Table 1) and will require greater vigilance and more widespread action for the population to reach and maintain sustainable levels.

Knowledge of the foraging range and feeding behaviour of all four species is needed to assess the importance of human-induced mortality factors at sea. With the apparent onset of climate change, further threats at sea are possible. Future population trends of each species will have to be viewed in the light of changing weather patterns, yet discerning the effects of climate change will always be difficult in species with populations that are either small or under rapid recovery. Any subtle decreases in breeding success brought about by gradual changes in climate may be swamped by the increases associated with successful recovery actions at their nesting grounds.

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REFERENCES

AINLEY, D.G.P.R., DEFOREST, L. & SPENCER, G. 1997. New insights into the status of the Hawaiian Petrel on Kauai. *Colonial Waterbirds* 20: 24-30.

AINLEY, D.G.P.R., DEFOREST, L., SPENCER, G. & NUR, N. 1995. The ecology of Newell's Shearwater and Dark-rumped Petrel on the island of Kauai. Final report task 2 to the Electric Power Research Institute, Palo Alto, CA.

BAKER, G.B., GALES, R., HAMILTON, S. & WILKINSON, V. 2002. Albatrosses and petrels in Australia: a review of their conservation and management. *Emu* 102: 71-97.

BANNERMAN, D.A. & BANNERMAN, W.M. 1965. Birds of the Atlantic Islands. Vol. 2: a history of the birds of Madeira, the Desertas, and Porto Santo Islands. Edinburgh: Oliver and Boyd.

BIRDLIFE INTERNATIONAL 2000. Threatened birds of the world. Barcelona & Cambridge: Lynx Edicions & BirdLife International.

BROTHERS, N.P., COOPER, J. & LØKKEBORG, S. 1999. The incidental catch of seabirds by longline fisheries: worldwide review and technical guidelines for mitigation. F*AO Fisheries Circular No. 937*. Rome: Food and Agriculture Organization of the United Nations.

BRYAN, W.A. 1908. Some birds of Molokai. *Occasional Paper B.P. Bishop Museum* 4: 43-86.

BUCKLE, A. & ZINO, F. 1989. Saving Europe's rarest bird. *The Roundel* 5: 112-116.

CONANT, S. 1980. Recent records of the Uau (Dark-rumped Petrel) and the Ao (Newell's Shearwater) in Hawaii. *Elepaio* 41: 1-3.

CROXALL, J.P. & PRINCE, P.A. 1994. Dead or alive, night or day: how do albatrosses catch squid? *Antarctic Science* 6: 155-162.

D'OMBRAIN, A.F. 1943. The Cabbage Tree Island colony in the 1941-42 season. *Emu* 42: 156-159.

D'OMBRAIN, A.F. 1970. Notes on the Gould Petrel. *Australian Bird Bander* 8: 82-84.

ENTICOTT, J. & TIPLING, D. 1997. Photographic handbook of the seabirds of the world. London: New Holland.

FULLAGAR, P.J. 1976. Seabird islands No. 35: Cabbage Tree Island, New South Wales. *Australian Bird Bander* 14: 94-97.

GOULD, J. 1844. *Procellaria leucoptera. Proceedings of the Zoological Society of London* 12: 57.

HARRIS, M.P. 1970. The biology of an endangered species the Dark-rumped Petrel (*Pterodroma phaeopygia*) in the Galapagos Islands. *Condor* 72: 76-84.

HARRISON, C.S., NAUGHTON, M.B. & FEFER, S.I. 1984. The status and conservation of seabirds in the Hawaiian Archipelago and Johnston Atoll. In: Croxall, J.P., Evans, P.G.H. & Schreiber, R.W. (Eds.). Status and conservation of the world's seabirds. *ICBP Technical Publication* No. 2. Cambridge: International Council for Bird Preservation. pp. 513-526.

HENSHAW, H.W. 1902. Birds of the Hawaiian Islands, being a complete list of the birds of the Hawaiian possessions, with notes on their habits. Honolulu: Thos. G. Thrum.

HINDWOOD, K.A. & SERVENTY, D.L. 1943. Further notes on *Pterodroma leucoptera*. *Emu* 42: 153-155.

HIRAI, L.T. 1978. Possible Dark-rumped Petrel colony on Lanai, Hawaii. *Elepaio* 38: 71-72.

HODGES, C.N. 1994. Effects of introduced predators on the survival and fledging success of the endangered Hawaiian Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*). MSc Thesis, University of Washington, Seattle.

HODGES, C.N. & NAGATA, R.J. JR 2001. Effects of predator control on the survival and breeding success of the endangered Hawaiian Dark-rumped Petrel. *Studies in Avian Biology* 22: 308-318.

HU, D. 1995. Annual endangered species report: Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*). Unpublished report to the U.S. Fish and Wildlife Service. Hawaii: Hawaii Volcanoes National Park.

HYATT, A.D., HINE, P.M., JONES, J.B., WHITTINGTON, R.J., KEARNS, C., WISE, T.G., CRANE, M.S. & WILLIAMS, L.M. 1997. Epizootic mortality in the pilchard Sardinops sagax neopilchardus in Australia and New Zealand in 1995. II. Identification of a herpesvirus within the gill epithelium. *Diseases of Aquatic Organisms* 28: 17-29.

IUCN 1994. IUCN Red List categories. Prepared by the IUCN Species Survival Commission. Gland, Switzerland & Cambridge, UK: The World Conservation Union..

JUVIK, C.P. & JUVIK, J.O. 1998. Atlas of Hawaii, third edition. Honolulu: University of Hawaii Press.

LAND, L.S. & MACKENZIE, F.T. 1970. Field guide to Bermuda's geology. Special Publication No. 4. Bermuda: Bermuda Biological Station for Research.

LEFROY, J.H. 1877. Memorials of the discovery and early settlement of the Bermudas or Somers Islands 1515-1652. Compiled from the colonial records and other original sources. Vol. 1. London: Longmans, Green and Co.

MATHEWS, G. 1934a. Remarks on the races of *Pterodroma mollis*. *Bulletin of the British Ornithologists' Club* 54: 178-179.

MATHEWS, G. 1934b. A check-list of the order Procellariiformes. *Novitates Zoologicae* 39: 151-206.

MAUL, G.E. 1965. The natural features and climate of the Madeira Archipelago. In: Bannerman, D.A. & Bannerman, W.M. (Eds.). Birds of the Atlantic Islands. Vol. 2: a history of the birds of Madeira, the Desertas, and Porto Santo Islands. Edinburgh: Oliver and Boyd. pp. 35-48.

MURPHY, R.C. & MOWBRAY, L.S. 1951. New light on the Cahow, *Pterodroma cahow*. *Auk* 68: 266-280.

NSW NATIONAL PARKS AND WILDLIFE SERVICE 2001. Gould's Petrel *Pterodroma leucoptera* approved recovery plan. Hurstville: NSW National Parks and Wildlife Service.

OLSON, S.L. & JAMES, H.F. 1982a. Fossil birds from the Hawaiian Islands: evidence for wholesale extinction by man before western contact. *Science* 217: 633-635.

OLSON, S.L. & JAMES, H.F. 1982b. Prodromus of the fossil avifauna of the Hawaiian Islands. *Smithsonian Contributions to Zoology* 365: 1-59.

PRIDDEL, D. & CARLILE, N. 1995a. An artificial nest box for burrow-nesting seabirds. *Emu* 95: 290-294.

PRIDDEL, D. & CARLILE, N. 1995b. Mortality of adult Gould's Petrels *Pterodroma leucoptera leucoptera* at the nesting site on Cabbage Tree Island, New South Wales. *Emu* 95: 259-264.

PRIDDEL, D. & CARLILE, N. 1997a. Boondelbah Island confirmed as a second breeding locality for Gould's Petrel *Pterodroma leucoptera leucoptera*. *Emu* 97: 245-248.

PRIDDEL, D. & CARLILE, N. 1997b. Conservation of the endangered Gould's Petrel *Pterodroma leucoptera leucoptera*. *Pacific Conservation Biology* 3: 322-329.

PRIDDEL, D. & CARLILE, N. 2001. A trial translocation of Gould's Petrel (*Pterodroma leucoptera leucoptera*). *Emu* 101: 79-88.

PRIDDEL, D., CARLILE, N., DAVEY, C. & FULLAGAR, P.J. 1995. The status of Gould's Petrel, *Pterodroma leucoptera leucoptera*, on Cabbage Tree Island, New South Wales. *Wildlife Research* 22: 601-610.

PRIDDEL, D., CARLILE, N. & WHEELER, R. 2000. Eradication of European Rabbits (*Oryctolagus cuniculus*) from Cabbage Tree Island, NSW, Australia, to protect the breeding habitat of Gould's Petrel (*Pterodroma leucoptera leucoptera*). *Biological Conservation* 94: 115-125.

RICHARDSON, F. & WOODSIDE, D.H. 1954. Rediscovery of the nesting of the Dark-rumped Petrel in the Hawaiian Islands. *Condor* 56: 323-327.

RYAN, P.G. & MOLONEY, C.L. 1988. Effect of trawling on bird and seal distributions in the southern Benguela Current. *Marine Ecology Progress Series* 45: 1-11.

SCHMITZ, E. 1905. Tagebuch-Notizen aus Madeira. *Ornithologisches Jahrbuch* 16: 219-226.

SIMONS, T.R. 1983. Biology and conservation of the endangered Dark-rumped Petrel (*Pterodroma phaeopygia sandwichensis*). CPSU/UW83-2. Seattle: National Park Service, Cooperative Park Studies Unit, University of Washington, Seattle.

SIMONS, T.R. 1985. Biology and behavior of the endangered Hawaiian Dark-rumped Petrel. *Condor* 87: 229-245.

SIMONS, T.R. & HODGES, C.N. 1998. Dark-rumped Petrel (*Pterodroma phaeopygia*). In: Poole, A. & Gill, F. (Eds.). The birds of North America, No. 345. Philadelphia: The Birds of North America. pp. 1-24.

SPEAR, L.B., AINLEY, D.G., NUR, N. & HOWELL, S.N.G. 1995. Population size and factors affecting at-sea distribution of four endangered procellariids in the tropical Pacific. *Condor* 97: 613-638.

VERRILL, A.E. 1902. The 'Cahow' of the Bermudas, an extinct bird. *Annals of the Magazine of Natural History* 7: 26-31.

WARHAM, J. 1990. The petrels: their ecology and breeding systems. London: Academic Press.

WETMORE, A. 1962. Notes on fossil and subfossil birds. *Smithsonian Museum Collections* 145: 15-17.

WINGATE, D. 1988. The restoration of an island ecology. *Whole Earth Review* Fall: 42-57.

WINGATE, D.B. 1978. Excluding competitors from Bermuda Petrel nesting burrows. In: Temple, S.A. (Ed.). Endangered birds: management techniques for preserving threatened species. Madison: University of Wisconsin Press. pp. 93-102.

WINGATE, D.B. 1985. The restoration of Nonsuch Island as a living museum of Bermuda's pre-colonial terrestrial biome. In: Moors, P.J. (Ed.). Conservation of island birds. *ICBP Technical Publication* No. 3. Cambridge: International Council for Bird Preservation. pp. 225-238.

WINGATE, D.B. 1995. Cahow update. *Bulletin of the Department of Agriculture and Fisheries, Bermuda* 66: 101-105.

WURSTER, C.F. & WINGATE, D.B. 1968. DDT residues and declining reproduction in the Bermuda Petrel. *Science* 159: 979-981.

ZIMMERMAN, D.R. 1975. To save a bird in peril. New York: Coward, McCann & Geoghegan.

ZINO, F. 1992. Cats amongst the Freiras. *Oryx* 26: 174.

ZINO, P.A. & ZINO, F. 1986. Contribution to the study of the petrels of the genus *Pterodroma* in the Archipelago of Madeira. *Boletin Do Museu Municipal Do Funchal* 38: 141-165.

ZINO, F., BISCOITO, M. & NEVES, H.C. 1989. Madeira Freira Project. A confidential report, circulated to active partners in the project. Madeira: Unpublished report, Freira Conservation Project.

ZINO, F., OLIVEIRA, P., KING, S., BUCKLE, A., BISCOITO, M., NEVES, H.C. & VASCONCELOS, A. 2001. Conservation of Zino's Petrel *Pterodroma madeira* in the archipelago of Madeira. *Oryx* 35: 128-136.

BREEDING AND FLEDGING BEHAVIOUR OF THE CHATHAM TAIKO (MAGENTA PETREL) *PTERODROMA MAGENTAE*, AND PREDATOR ACTIVITY AT BURROWS

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SUMMARY

JOHNSTON, R.B., BETTANY, S.M., OGLE, R.M., AIKMAN, H.A., TAYLOR, G.A. & IMBER, M.J. 2003. Breeding and fledging behaviour of the Chatham Taiko (Magenta Petrel) *Pterodroma magentae*, and predator activity at burrows. *Marine Ornithology* 31: 193-197.

Breeding and fledging activity of the Chatham Taiko or Magenta Petrel *Pterodroma magentae* were observed from October 2000- May 2001 during 3696 h of video surveillance at 16 burrows. Additional video-monitoring was done during 1999/2000 (486 h), 2001/02 (703 h) and 2002/03 (590 h). Laying in one burrow, and incubation changeovers in three, were observed. Three chicks were fed on average every 3.86 days (March-April) until the desertion period. Parental visits, shared equally by the sexes, lasted 33 minutes - 26.3 h, and ceased between 22 April and 9 May, causing desertion periods averaging 16 days (range 9-23 d, n=6). Five chicks first emerged on 21 April-1 May. Time chicks spent outside the burrow increased approaching fledging, while wing-flapping rate increased, then decreased. Mean fledging date was 15 May (range 6-27 May, n=18). Desertion periods were longer on the leeward side of the colony (mean 22 days, n=3) than on the windward side (mean 11 days, n=3), and more leeward fledglings crashed attempting to leave (75% vs 33%). Rats (Black *Rattus rattus* &/or Polynesian *R. exulans*) were the only predators observed on video. All 38 recorded rat visits seemed benign, although 63% involved burrow entry, but visitation rate was highest in April when chicks were large.

Keywords: Chatham Taiko, Magenta Petrel, *Pterodroma magentae*, Chatham Island, video-monitoring, breeding behaviour, chick-rearing, fledgling behaviour, rats

INTRODUCTION

Endemic to Chatham Island, New Zealand, the Critically Endangered Chatham Taiko or Magenta Petrel *Pterodroma magentae* is one of the world's rarest seabirds (Heather & Robertson 1996) with a total population estimated at 100-150 birds (Taylor 2000, Aikman *et al*. 2001). It is a moderately large (c. 475 g), white-bellied gadfly petrel, summer-breeding in and restricted to the South Pacific near the Subtropical Convergence and to sub-Antarctic seas. Taiko are now known to breed only in forest 4-6 km inland, in and near the Manuel & Evelyn Tuanui Nature Reserve around the Tuku-a-tamatea (Tuku) River and a tributary in south-west Chatham Island (44º 04'S, 176º 36'W). The upper Tuku Valley, which holds most Taiko burrows, runs SSW, so that numerous burrows on its west side are to leeward of the prevailing NW-SW winds. This had implications for departing fledglings there.

Between October 2000 and May 2001 video-monitoring of Taiko breeding activity was undertaken at burrows in Tuku Valley. The specific objectives were to:

1. Determine the identity of Taiko visiting each burrow by colour bands, if present,
2. Observe incubation behaviour,
3. Determine feeding patterns during chick-rearing,
4. Establish dates of first emergence and departure by fledglings, and
5. Record visits to burrows, and activity, by potential predators.

Feral Domestic Cats *Felis catus*, Wekas *Gallirallus australis*, Australian Possums *Trichosurus vulpecula* and Black Rats *Rattus rattus* and Polynesian Rats *R. exulans* were commonly found in the area where Taiko breed and often close to burrows (Imber *et al*. 1994, Ogle 2002). Predator control measures included leg-hold traps at baited or walk-through sites, well away from burrows, for larger predators; for rats, poison bait stations and Victor® and Easiset® snap-traps in the vicinity of burrows; and Fenn® traps (in protective cages) for Wekas and rats, near but not close to burrows (Ogle 2002).

Burrows have been monitored by direct observations and entrance fencing, in conjunction with predator control, since 1987 (Imber *et al*. 1994). For the first time, in the 1999/2000 season, video-monitoring was used intermittently at four breeding burrows. This 2000/01 study reports the findings of the most intensive Taiko video surveillance undertaken. We know of no other study of burrowing petrels by video-monitoring reported in the literature.

METHODS

Camera equipment

Two types of camera were used: entrance cameras (three sets) for recording activity around the burrow entrance and chamber cameras (two sets) for recording activity on the nest. Each entrance set comprised a video camera (low resolution, black and white, infrared-sensitive security camera in a custom-made waterproof housing), connected to a Panasonic Ag1070DCE 24-h time-lapse video recorder (VCR) by a c.12-m cable, and a custom-made light unit with banks of infrared, light-emitting diodes (SFH415T). The two chamber camera sets consisted of a black and white 420-line pinhole camera with five infrared light-emitting diodes for lighting, connected to a VCR outside the burrow. A Dryfit® 12v/36Ah battery powered each unit.

Entrance fence monitoring

Burrow entrances were monitored throughout the breeding season with the use of fences (small sticks spaced across the entrance). Fences were checked at least weekly from the beginning of the breeding season (early September) until burrows with hatchlings were identified by burrow-scoping, or continued burrow activity, in February. Observations in past seasons showed that most non-breeders ceased visiting in late January. Burrows were then checked every second day, and finally almost daily during the late chick-rearing and fledgling emergence phases (late April – May).

Camera set-up

Entrance fence monitoring early in the season indicated active burrows. Cameras were set up 1-2 m from burrow entrances by tying them to nearby tree trunks or stakes. To identify banded adults the camera was placed level with the top of the entrance mound, and at 45º to the entrance. During chick emergence the camera was moved back to extend the field of view around the burrow entrance. Burrows were illuminated at night by an infrared light positioned beside the camera, usually on the same tree, and directed into the burrow entrance. To ensure minimal risk to birds, potential routes used by Taiko, for landing and walking to take-off sites, were avoided when positioning all components of the video-recording unit.

Chamber cameras were inserted through black plastic piping of 30-mm internal diameter that had previously been installed into the vacant nest chamber utilizing a study hole. The pre-focused camera was positioned at the very end of the tubing to prevent reflection. The camera was anchored within the piping using insulation tape and the study hole lid well secured in place. The VCR and battery were positioned outside the burrow and away from possible Taiko routes.

The burrow camera was monitored nightly or continuously with the VCR on the 24-h time-lapse mode (5.55 frames/s). Videotapes were changed daily. For the entrance camera, the VCR was set to run from just before dusk to just after dawn, usually on the 12-h mode (10 frames/s). Normal speed is 50 frames/s. Videotapes were changed daily, but every second day if 24-h mode was used. Date, time and record mode were superimposed on the recorded picture.

Videotape viewing

All videotapes were viewed from start to finish on fast-forward mode but, when a Taiko or predator was seen, tapes were viewed at normal speed. Because rats may move very quickly through the camera field on fast-forward, the viewer might miss them. Therefore, two videotapes per month from each of the three main groups of burrows were watched at normal speed to count predator visits accurately (compared to fast-forward, no difference was measurable). Taiko and predator video footage were transcribed onto activity log sheets from which the hours of recording, number of birds per night and number of predators per night could be calculated.

Identification of individual Taiko was possible from black and white colour band and numbered metal band combinations, with no more than two bands per leg. These were put on the birds when captured at the burrows, on the ground nearby, or at the light station in the lower Tuku Valley where many were originally caught (Crockett 1994). Tail-mounted, 2-g transmitters were taped to all fledglings when they began to emerge to trace those that crashed in the forest when attempting to depart, so that they could be returned to their burrows when found next day, or taken to the coast after two to four crashes.

Video-monitoring coverage

Sixteen burrows were video-monitored from October 2000 to May 2001, totaling 3696 h (850 h chamber, 2846 h entrance). The number of video hours at any one burrow ranged from 20-764 h. Effective recording hours and the month of recording differed between burrows depending on the birds' activity, the timing of camera set-up and removal, and technical problems. Most coverage was during December and January (incubation). Chamber cameras were used at two burrows only during incubation. April (late chick-rearing) and May (fledgling emergence and departure) also received a relatively high coverage.

Additional entrance monitoring was done in 1999/2000 (four burrows, December-February, 486 h) and in 2001/02 (four burrows, April-May, 703 h) (M. Ogle unpubl. data), and in 2002/03 (11 burrows, September-October, 590 h) (H. Schlumpf unpubl. data).

RESULTS

Adult identity and activity

Taiko identity was confirmed at 12 of the 16 burrows monitored by video in 2000/01. At five burrows only one adult bird was identified as present (four males and one female). No breeding occurred at

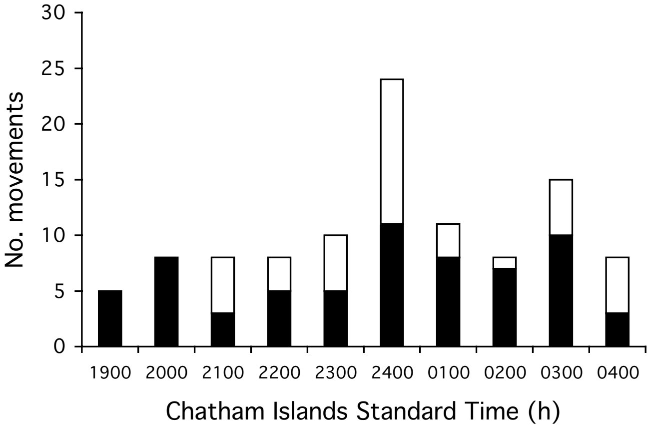

Fig. 1. Activity of breeding (shaded) and non-breeding (clear) Chatham Taiko at burrow entrances on Chatham Island during October-April 2000/01 by hour of night. Includes entries and exits, but repeated movements in and out by the same bird were recorded as only one movement.

any of these. The identity of breeding birds was confirmed at six of the 10 burrows where eggs were laid.

Adult activity from October to April, as measured by appearances (entry or exit) at burrow entrances, occurred throughout the night (Fig. 1), both for breeders and non-breeders. We observed no indication that the video equipment and infrared light disturbed the birds' behaviour.

Incubation behaviour

A chamber camera was first installed on 14 November 2000, when the burrow was unoccupied. Video surveillance was carried out every second night from 22-28 November, and then nightly until 22 December (356 h of observations) (Table 1). The female was first recorded on 26 November, one hour after full darkness, and laid after 54 minutes of nest preparation and 11 minutes out of camera view. On 30 November the male arrived 1.5 h after full darkness. There was a decrease in activity, notably of repositioning egg or body and preening, as his 16-day shift progressed (Table 1). The second incubation changeover on 16 December was completed within 6 minutes. Video-monitoring continued for a further five nights and the female incubated for at least 10 days. Times off the egg would be mainly to defaecate outside the burrow, or to gather nest material.

TABLE 1
Behaviour of a pair of incubating Chatham Taiko from 26 November (egg-laying) to 21 December 2000, expressed as the number of times each act was initiated, as observed during nightly video surveillance

Date	Sex	Reposition egg or body	Move material	Leave egg unattended	Preen
26 Nov.	F lays	0	3	0	0
27 Nov.	F	no obs.	no obs.	no obs.	no obs.
28 Nov.	F	2	1	0	1
29 Nov.	F	6	0	0	15
30 Nov.	F	7	3	0	8
	M	3	2	0	0
1 Dec.	M	6	0	0	3
2 Dec.	M	7	0	0	14
3 Dec.	M	9	1	0	11
4 Dec.	M	5	0	0	4
5 Dec.	M	3	1	2	5
6 Dec.	M	1	0	1	7
7 Dec.	M	1	1	0	2
8 Dec.	M	3	1	0	0
9 Dec.	M	1	0	0	0
10 Dec.	M	1	0	0	1
11 Dec.	M	0	0	0	1
12 Dec.	M	0	0	0	2
13 Dec.	M	0	0	0	1
14 Dec.	M	3	2	0	3
15 Dec.	M	0	0	0	1
16 Dec.	M	1	0	0	1**
	F	3	2	0	1**
17 Dec.	F	3	1	0	1
18 Dec.	F	1	0	0	2
19 Dec.	F	5	2	1	2
20 Dec.	F	0	0	0	1
21 Dec.†	F	1	0	0	3

**Mutual preening

At a second burrow, monitored almost continuously (434 h) from 15 January–6 February, the final changeover (male-female) on 16 January at 24h00, taking only a few minutes, should have almost coincided with hatching (laying *c*. 25 November, incubation *c*. 53 days). However, the embryo had died in late incubation, so the information obtained thereafter was of little value. She left after four days of erratic incubation. The male returned after 10 days, which would perhaps normally have been his first chick-feeding visit. He incubated for 10 days till he also departed.

An entrance camera at a third burrow was run from 29 December-21 January. On 31 December, and 4 and 9 January an adult (probably the female) came out briefly to collect nest material around the entrance, or to excrete. The only change-over during this period was on 12 January.

Parental visits during chick-rearing

The only video recording in February at a successful breeding burrow was at a burrow during early chick-rearing. All three recorded visits over seven nights (31 January-7 February) were by the female. However, she stayed over on two days, so the chick was effectively visited and probably fed on five nights (0.71 visits/night). Subsequent observations showed a decrease in the frequency of chick-feeding visits from March to April as chicks grew (Table 2). There was no difference between the sexes in the frequency of visits. Time adults spent at the burrow during a single visit ranged from 33 minutes to 26.3 h. The average time for five male visits was 174±149 minutes (range 33-350 minutes), and for eight female visits it was 193±117 minutes (range 67-415 minutes). These determinations exclude visits where the adult stayed over during the day. The longest intervals between feeds were 11 days in March (detected by fencing), and 17 days in April (from video monitoring).

Parental visits occurred at any time of night but with a concentration in the first three hours of darkness. Of 18 timed visits, eight were during the period 18h00-21h00, four during 21h00-24h00, three during 24h00-03h00 and three during 03h00-05h00. The last visits were between 22 April and 9 May (mean 29 April) in 2001 (n=3) and 2002 (n=3).

TABLE 2
Parental feeding visits of Chatham Taiko during late chick-rearing in 2000/01, observed by video-monitoring of burrow entrances

Month	Burrow	Hours recorded	Number of nights	Number of visits	Visits /night	Female visits	Male visits
March	A	112	12	4	0.33	3	1
	B	85	9	4	0.44	2	2
April	A	180	20	2	0.10	1	1
	B	145	20	6	0.30	4	2
	C	179	20	5	0.25	1	4
Total		**701**	**81**	**21**	**0.26**	**11**	**10**

Fledgling behaviour

The dates of first emergence of five chicks (three in 2001, two in 2002) ranged from 21 April to 1 May (mean 25 April). For the three chicks intensively observed in 2001, there was an increase in time spent outside the burrow each night as they approached fledging, but behaviour varied. One remained inside the burrow for about half of each night until four nights prior to fledging. Another was regularly spending over half of each night outside the burrow in the 2.5 weeks before fledging. The frequency of wing exercising increased, then decreased. The highest rate of wing-stretching and flapping was by the chick that fledged first.

At the beginning of the emergence period, time of first exit was generally during the period 24h00-02h00 for all chicks. As two of the chicks approached fledging, both began emerging earlier (eventually during 17h00-20h00). In contrast, the third chick continued to emerge much later; often from 01h00-02h00, until departure.

Fledging dates of 18 chicks (six in 2000, five in 2001, seven in 2002) were 6-27 May (mean 15 May). Desertion periods were 9-23 days (mean 16 days, n=6). Of 18 fledglings studied (2000-2002), 61% failed their initial fledging attempt and were rescued next day from the forest. Three fledglings from the leeward side of Tuku Valley had desertion periods of 22 days (range 22-23) compared to the 11 days (range 9-12) of three in windward sites (data available for 2001 and 2002 only). Their times from first emergence to departure were also longer (24 and 27 days vs 16 days for the windward fledgling, 2001 data). The former were also more likely to be rescued (75% of 12 vs 33% of six).

Predator visits to Taiko burrows

Rats were the only predators observed, and were recorded at six of the 16 burrows under intermittent surveillance from October - May 2000/01, including all three with chicks. No effects of rats on Taiko adults, chicks or eggs were observed.

Twenty-five rat visits were recorded during 2846 h of video surveillance, or 0.009 visits/h (Table 3). Median time per visit was 61 s; 72% lasted less than one minute. The majority of visits occurred between 19h00-21h00, and 52% involved burrow entry. Rat visitations were highest in April. Late November through February (egg to early chick stages) is the period of Taiko vulnerability to rat predation, late January–early February being the most vulnerable time when chicks have just hatched and are alone most of the time. Only one rat visit in 487 h was recorded in January-February 2001 (0.002/h).

TABLE 3
Frequency (visits/h) of rat visits and entries to ChathamTaiko burrows, as observed by video-monitoring during the breeding season, October-May 2000/01

Month	Hours of observation	Number of rat visits	Rat visits/h	Mean visit length(s)	Number of entries
October	331	1	0.003	51	0
November	316	0	0	0	0
December	374	3	0.008	138	3
January	401	1	0.003	89	1
February	86	0	0	0	0
March	294	3	0.010	199	2
April	505	12	0.024	31	6
May	539	5	0.009	27	1
Total	**2846**	**25**	**0.009**	**61**	**13**

However, from December 1999 to February 2000 there were 0.027 rat visits/h (486 h), suggesting that rat numbers were higher that breeding season. In the 2002/03 season, 590 h of video observations during late September-October. showed only one rat visit (0.002/h), similar to the 2000/01 rate for October (Table 3).

DISCUSSION

Video monitoring of Taiko burrows was a valuable means of identifying individually colour-banded birds, and observing activities (incubation changeovers, parental visits, fledgling emergence, predator visits) with minimal disturbance of the birds. The main challenge in band identification was getting a clear still frame of each leg, and distinguishing between shiny metal and white bands in the black-and-white picture.

Incubation

The incubation pattern in Taiko seems essentially identical to that in Grey-faced Petrels *Pterodroma macroptera gouldi* (Imber 1976, Johnstone & Davis 1990), and Cook's Petrels *P. cookii* (Imber *et al*. 2003), and probably is the general pattern in this genus. After laying the female incubates for a few days until relieved by the male, or he takes over immediately. Most of incubation is then achieved in three main spells of about equal length (male-female-male), with hatching about the end of this. Females usually hatch, briefly guard and feed the hatchling. The three visits by a female Taiko during 1-6 February to her young chick were consistent with this.

Chick-feeding

Results, based on only three observed burrows, were insufficient to be conclusive. The low feeding rate in April was largely due to 16 nights without a feed to one chick whose male parent made only two visits in 32 nights. He disappeared late next season. Thus there may not usually be such a decrease in the feeding rate from March to April.

Fledgling behaviour from emergence to departure

The aerodynamic problem affecting fledglings from burrows on the leeward side of Tuku Valley delayed their attempts to leave, as they searched for suitable take-off sites or awaited favourable wind. They were then more likely to crash when attempting to depart. Their desertion periods of up to 23 days, and intervals from first emergence to departure of up to 27 days, are unusually long for a petrel (MJI, GAT pers. obs.). Leeward fledglings in Tuku Valley will need to continue to be monitored carefully, to ensure that they depart without excessive delay and in good condition.

Predators

Despite the network of poison stations and traps, a few rats managed to visit burrows but no actual predation incidents were detected. Significantly, no rat visits were seen during 16 January-10 February in 2001, the period when petrels are most vulnerable (undefended hatchlings). Video observations in 1999/2000, 2001/02 and 2002/03 also showed rats to be the only predators visiting burrows, and that Taiko were unharmed in the particular periods observed. The peak of rat numbers seen in April corresponds with the characteristic, autumnal, post-breeding peak of rodent numbers in New Zealand (pers. obs.). However, cessation of rat trapping in early April may also have contributed to this peak of sightings.

Feral cats are possibly the predator most dangerous to Taiko, especially for fledglings emerging from burrows. As yet no cats have been observed on video but the potential threat is still there, as 69 cats were trapped in the area throughout the 2000/01 season (Ogle 2002). A Taiko humerus only a few years old, found near a breeding burrow in 2001, in an area that had no trapping until 2000 when burrows were found there, seemed to bear signs of cat predation (A.J.D. Tennyson pers. comm.).

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REFERENCES

AIKMAN, H., DAVIS, A., MISKELLY, C., O'CONNOR, S., & TAYLOR, G. 2001. Chatham Islands threatened birds. Threatened species recovery plan 36: Chatham Island Taiko recovery plan 2001-2011. Wellington: New Zealand Department of Conservation. 23 pp.

CROCKETT, D.E. 1994. Rediscovery of Chatham Island Taiko *Pterodroma magentae*. *Notornis* 41 (Supplement): 49-60.

HEATHER, B.D. & ROBERTSON, H.A. 1996. The field guide to the birds of New Zealand. Auckland: Viking.

IMBER, M.J. 1976. Breeding biology of the Grey-faced Petrel *Pterodroma macroptera gouldi*. *Ibis* 118: 51-64.

IMBER, M.J., TAYLOR, G.A., GRANT, A.D. & MUNN, A. 1994. Chatham Island Taiko *Pterodroma magentae* management and research, 1987-1993: predator control, productivity, and breeding biology. *Notornis* 41 (Supplement): 61-68.

IMBER, M.J., WEST, J.A. & COOPER, W.J. 2003. Cook's Petrel (*Pterodroma cookii*): historic distribution, breeding biology and effects of predators. *Notornis* 50: 221-230.

JOHNSTONE, R.M. & DAVIS, L.S. 1990. Incubation routines and foraging-trip regulation in the Grey-faced Petrel *Pterodroma macroptera gouldi*. *Ibis* 132: 14-20.

OGLE, M. 2002. Chatham Island Taiko final report 2000/2001. Unpubl. report. Chatham Islands Area Office, New Zealand Department of Conservation. 15 pp.

TAYLOR, G.A. 2000. Action plan for seabird conservation in New Zealand. Part A: threatened seabirds. *Threatened species Occasional Publication* 16. Wellington: New Zealand Department of Conservation.

FISH PREY OF THE BLACK SKIMMER *RYNCHOPS NIGER* AT MAR CHIQUITA, BUENOS AIRES PROVINCE, ARGENTINA

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SUMMARY

MARIANO-JELICICH, R., FAVERO, M. & SILVA, M.P. 2003. Fish prey of the Black Skimmer *Rynchops niger* at Mar Chiquita, Buenos Aires Province, Argentina. *Marine Ornithology* 31: 199-202.

We studied the diet of the Black Skimmer *Rynchops niger* during the non-breeding season (austral summer-autumn 2000) by analyzing 1034 regurgitated pellets from Mar Chiquita, Buenos Aires Province, Argentina. Fish was the main prey, with five species identified: *Odontesthes argentinensis*, *O. incisa*, *Anchoa marinii*, *Engraulis anchoita* and P*omatomus saltatrix*. *O. incisa* and *O. argentinensis* were present in all the sampled months, showing also larger values of occurrence, numerical abundance and importance by mass than other items. The average size of the fish was 73±17 mm in length and 2.2±1.7 g in mass. Significant differences were observed in the comparison of the occurrence, importance by number and by mass throughout the study period. The presence of fish in the diet of the Black Skimmer coincides with a study carried out on the North American subspecies. Our analysis of the diet suggests that skimmers use both estuarine and marine areas when foraging.

Keywords: Black Skimmer, *Rynchops niger*, Argentina, South America, diet

INTRODUCTION

Black Skimmers *Rynchops niger* are known by the morphological characteristics of the bill and their particular feeding technique, skimming over the water surface to catch fish and other prey. Despite available information on their breeding biology (Erwin 1977a, Burger 1982, White *et al*. 1984) and feeding ecology (e.g. Erwin 1977b, Black & Harris 1983, Burger & Gochfeld 1990), only general descriptions of the diet are given, with no extensive quantitative analysis (see Zusi 1996). Earlier investigators described skimmers feeding in shallow pools and streams with calm water (Erwin 1977b, Black & Harris 1983). They also reported skimmers to be restricted in their habitat use, feeding almost exclusively in marsh channels and tide pools, with open waters occasionally used (Erwin 1977b). Coincidentally, their diet consisted mainly of small inshore fish species, while marine fish species were less important (Erwin 1977a,b, Black & Harris 1983, White *et al*. 1984). All these earlier works were carried out in North America during the breeding season (see Black & Harris 1983). Recent studies (Favero *et al*. 2001) undertaken in southern South America (Buenos Aires Province, Argentina) during the non-breeding season, showed an alternate use of foraging areas by these birds, consuming both estuarine and marine fish prey. Thus, Black Skimmers may be more plastic in their habitat use during the non-breeding season (Favero *et al*. 2001). In this study, we provide additional detailed information on the diet of non-breeding Black Skimmers at Mar Chiquita coastal lagoon, the only coastal lagoon along the Argentine shore.

METHODS

Study area

We studied the diet of Black Skimmers by analyzing 1034 regurgitated pellets collected from roosting sites between February and May 2000 at Mar Chiquita coastal lagoon (37º 40'S, 57º 22'W), Buenos Aires Province, Argentina. During the austral summer-autumn from 5000 to 10 000 Black Skimmers (by far the most abundant seabird species) roost in Mar Chiquita, which is the most important wintering area in Argentina.

Field procedures and analyses

Diet was studied by analyzing regurgitated pellets. Once collected, each sample was dried at ambient temperature, dissected and the hard remains were identified using a stereomicroscope (20–60). Fish otoliths were identified to species using descriptions and illustrations from the literature (Torno 1970, Vilela 1988) and reference material from our own collections. Otoliths were separated into right and left, and the most abundant was considered as representing the number of fish prey of each species in the sample. The total length and width of otoliths was used to estimate the fish size (total length) and mass by regression equations used in previous studies (Favero *et al*. 2000a,b, Favero *et al*. 2001). Urostyles found in samples were also used for prey identification. The urostyles were separated into two types by using reference material in our own collection: "atheriniform (Atherinidae) type" and "clupeiform (Engraulidae and Clupeidae) type". Individuals belonging to each type were assigned to species accordingly to the proportion by number observed by the otoliths. The importance of prey categories was quantified as: (1) frequency of occurrence (F%), which is the percentage of samples in which a particular food type appeared, (2) numerical abundance (N%) as the percentage of prey items of one type out of all prey items, and (3) importance by mass (W%) as the percentage of biomass provided by one prey item out of the total biomass consumed (Duffy & Jackson 1986, Rosenberg & Cooper 1990).

Data analysis

The composition of the diet was compared throughout the samples by chi-square tests (χ^2). The prey sizes and masses estimations at the different samplings were compared by ANOVAs (F) and by Tukey post-hoc comparisons. In all cases we followed the statistical methods proposed by Underwood (1997) and Zar (1999). The degrees of freedom of the mentioned tests are given as sub-indices. Comparisons through the breeding season were performed by using month as the unit size.

RESULTS

Fish was the main prey in the diet (n = 98%), followed in importance by insects (1.1%, mainly coleoptera), crustaceans (0.5%, decapods, amphipods and isopods), molluscs (0.2%, cephalopods and gasteropods) and chelicerates (0.1%, aracnids). The overall comparison of the diet throughout the sampling period showed significant differences both in the occurrence ($\chi^2 = 116.74$, $P < 0.0001$) and the importance by number ($\chi^2 = 47.57$, $P < 0.0001$). Thirty-eight percent (n = 396) of the pellets analyzed contained otoliths; other samples contained fish bones and scales only. A total of 1680 fish prey was identified to species level from otoliths and bone remains. From 740 otoliths identified to species, 423 of them were measured and used to calculate prey size and mass.

Identified fish prey corresponded to the following species: “Pejerrey” Silverside *Odontesthes argentinensis*, “Cornalito” Silverside *Odontesthes incisa*, Marini’s Anchovy *Anchoa marinii*, Argentine Anchovy *Engraulis anchoita* and Bluefish *Pomatomus saltatrix* (Table 1). The first is considered an estuarine fish whereas the others are marine species (Rico 2000, Cousseau *et al*. 2001). Cornalito Silverside and Pejerrey Silverside were the most frequent prey and the most important by number and mass. Marini’s Anchovy and Argentine Anchovy were less frequent and important by number but accounted together for more than 19% by mass (Table 1). Argentine Anchovy, Bluefish and the unidentified items had values of importance by number lower than 2%.

Significant differences were observed in the comparison of the frequency of occurrence ($\chi^2 = 68.81$, $P < 0.0001$), numerical abundance ($\chi^2 = 233.86$, $P < 0.0001$) and importance by mass ($\chi^2 = 289.15$, $P < 0.0001$) of fish prey observed throughout the study. Silversides were present in all the sampled months, whereas Marini’s Anchovy and Argentine Anchovy were only present in samples from February and March (Fig. 1a, b).

Fish prey averaged 73±17 mm in length (range 25.6-127.5 mm, n = 423), and 2.2±1.7 g in mass (range 0.1-11.6 g, n = 423). The average size (total length) of consumed fish varied significantly through the study period ($F_{3,419} = 4.04$, $P < 0.01$), with smaller sizes observed in February (70.4 mm) and larger ones in April (78.8 mm). The differences observed in the size of Pejerrey Silversides consumed through the season (ANOVA $F_{3,175} = 4.75$, $P < 0.005$) were due to a significant increase of the sizes taken in April (Tukey $P < 0.05$) (Fig. 2a). In the case of Cornalito Silverside the differences were the result of the progressive increase of the sizes consumed through the study period ($F_{3,201} = 12.58$, $P < 0.0001$) (Fig.

TABLE 1

Frequency of occurrence (f%), numerical abundance (n%) and total length of fish prey in the diet of the Black Skimmer *Rynchops niger* at Mar Chiquita, Argentina

Species	F%[a]	N%[b]	W%	Total length (mm) Mean ± sd	Range
Cornalito Silverside *Odontesthes incisa*	46.7 (185)[c]	48.6 (816)[d]	38.7	67.5 ± 15.3 (205)[d]	25.9 - 113.5
Pejerrey Silverside *Odontesthes argentinensis*	40.9	38.2 (162)	39.3 (642)	75.2 ± 14.9	45.4 - 127.5 (179)
Marini’s anchovy *Anchoa marinii*	9.09 (36)	9.6 (161)	16.8	89.3 ± 22.8 (31)	25.6 - 122.5
Argentine Anchovy *Engraulis anchoíta*	2.02 (8)	1.8 (31)	2.5	71.8 ± 21.3 (7)	48.9 - 102.7
Bluefish *Pomatomus saltatrix*	0.5 (2)	0.1 (2)	2.0	101 (1)	-
Unidentified fish	7.07 (28)	1.6 (28)	?	-	-

a. Only considering samples containing otoliths (n = 396).
b. Including samples containing otoliths and/or bones (n = 1680).
c. Number of samples.
d. Number of fish-prey.

2b). The same trend was observed while considering the average mass variations of Pejerrey and Cornalito Silversides ($F_{3,175} = 12.47$, $P < 0.0001$, $F_{3,201} = 12.57$, $P < 0.0001$, respectively). Despite the low importance by number of Anchovy, the importance by mass during February and March reached the values observed in both silverside species (Fig. 1b). These large asymmetries between the importance by number and mass were related to the larger mass/length ratio observed in anchovies (0.061 g. cm^{-1}) in respect to those observed in silversides (0.037 and 0.039 g. cm^{-1}) (R.M-J. unpubl. data).

In this study, the number of fish prey per sample estimated by using otoliths (0.7±1.1) was significantly smaller than the number based on urostyles (1.4±1.2) (paired $t = 16.6$, df = 1033, $P < 0.0001$), thus accounting for some loss of information. However, some of these differences could be mediated by the large number of samples analyzed and the fact that the number of meals represented in one regurgitated pellet may be higher than those represented in other kind of samples, such as stomach contents or the observation of prey delivered to chicks (Casaux *et al*. 1997, 1998). Regardless of the possible methodological problems, regurgitated pellets are useful for the identification of individual food items consumed and for studying seabird diets during the non-breeding season (Brown & Ewins 1996). Preliminary results of the estimation of the minimum sample size needed to get accurate information about the diet of Black Skimmers showed that in the case of important prey (silversides in this study), samples larger than 150 pellets are enough to fit into 95% confidence interval of their importance by number. However, results should be carefully considered when considering less important prey such as clupeiform species (minimum sample size >400) (R. Mariano-Jelicich unpubl. data). The contrasting occurrence of clupeiform prey in the diet could be linked with seasonal migration patterns reported for these fish species in the area (Cousseau & Perrota 1998). In spite of the fact that an under-representation of soft-bodied prey is also suspected, this is probably unimportant because this prey type was low in previous studies (Leavitt 1957, Erwin 1977a; 1977b, Black & Harris 1983, Robert *et al*. 1989, Burger & Gochfeld 1990).

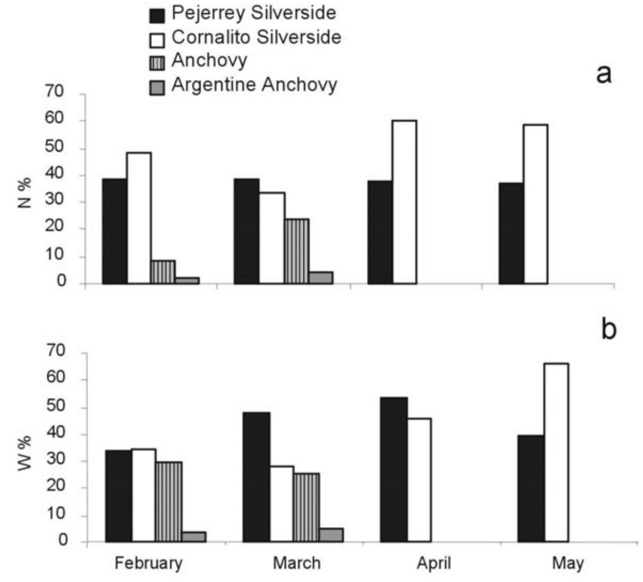

Fig. 1. Importance by number (a) and by mass (b) of the main prey in the diet of the Black Skimmer at Mar Chiquita, Argentina.

DISCUSSION

These results are similar to North American studies of the diet of the Black Skimmer, in which one of the most important prey was the silverside *Menidia* sp. (Atherinidae), whereas Anchovy and Bluefish were reported as occasional prey (Erwin 1977a,b). The only reference in areas reasonably close to the study area (200 km distance) comes from Punta Rasa, the southern tip of Samborombón Bay, Argentina (Favero *et al*. 2001) where the diet of skimmers was much more diverse (12 fish prey species, n = 642) than that observed in this work (five species, n = 1034). Both silversides were the most important fish prey in the diet in Mar Chiquita, whereas in Samborombon the main prey (in order of abundance) were Marini's Anchovies, White Croakers *Micropogonias furnieri*, Pejerrey Silversides, Argentine Anchovies and Cornalito Silversides (Favero *et al*. 2001). These differences in prey diversity might be partially related to the large fish diversity reported for Samborombón Bay (35 fish species, Lasta 1995), as compared to Mar Chiquita (28 species, Cousseau *et al*. 2001).

The average length of the prey consumed by Black Skimmers at Mar Chiquita was very close to the average length found in the diet of skimmers at nearby areas such Samborombon Bay (77±34 mm) (Favero *et al*. 2001). However, these data differed from the North American studies that reported an average prey length of 55 mm at Florida (Leavitt 1957), and between 10 and 50 mm at colonies from Virginia (Erwin 1977b). Since these previous studies are referred to

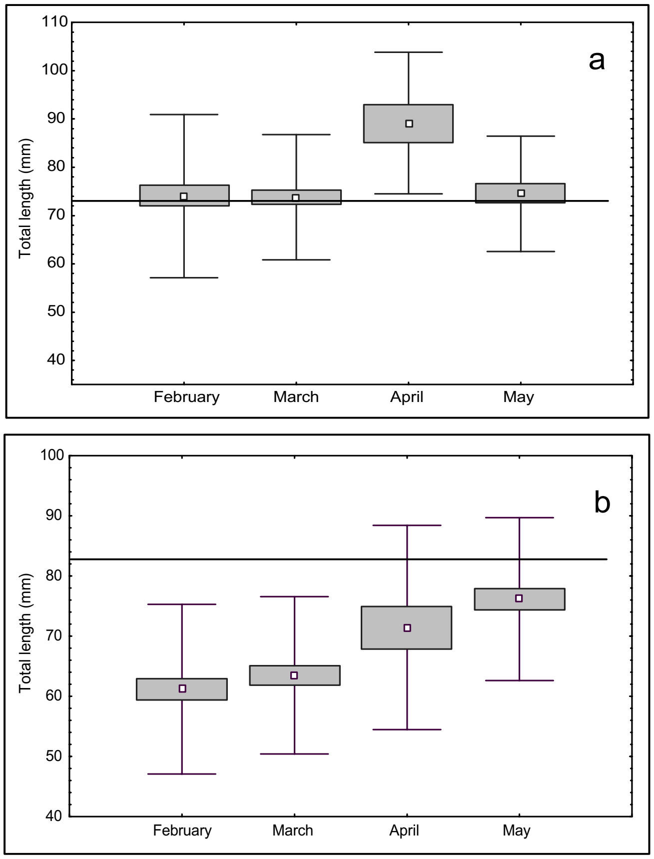

Fig. 2. Variation in the total length of Pejerrey (a) and Cornalito Silversides (b) consumed through the season by Black Skimmers. Means (dots) are shown together with ± one SE (boxes) and ± one SD (whiskers). Lines show median prey sizes (estimated on the basis of size ranges) reported by Cousseau *et al*. (2001)

prey found in stomachs or brought to the chicks, these differences in the sizes could be due to different sampling methods, seasonal variations of the diet, geographic differences, or to a combination of these.

The small proportion of samples with otoliths give rise to some uncertainty about the accuracy of the methodology (i.e. how well the recovered otoliths accurately reflected the fish consumed). Biases due to the loss by digestion and/or loss of the otoliths through the gastrointestinal tract can produce an important underestimate of fish larvae or small juvenile fish consumed (Duffy & Laurenson 1983, Jobling & Breiby 1986, Johnstone *et al*. 1990). These biases have been experimentally demonstrated in feeding trials on several bird species (Duffy & Laurenson 1983, Johnstone *et al*. 1990, Casaux *et al*. 1995).

Our results were consistent with previous studies carried out in Buenos Aires Province (Favero *et al*. 2001), showing that Black Skimmers in their non-breeding grounds feed both in fresh-water, estuarine and marine habitats, and are not restricted to foraging in estuarine and fresh-water environments as reported for breeding areas in the northern hemisphere. Further studies focused on the foraging behaviour of this species will allow a better understanding about foraging plasticity and constraints linked with their stereotyped foraging behaviour.

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REFERENCES

BLACK, B.B. & HARRIS, L.D. 1983. Feeding habitat of Black Skimmers wintering on the Florida Gulf coast. *Wilson Bulletin* 95: 404-415.

BROWN, K.M. & EWINS, P.J. 1996. Technique-dependent biases in determination of diet composition: an example with Ring-billed Gulls. *Condor* 98: 34-41.

BURGER, J. 1982. The role of reproductive success in colony-site selection and abandonment in Black Skimmers (*Rynchops niger*). *Auk* 99: 109-115.

BURGER, J. & GOCHFELD, M. 1990. The Black Skimmer: social dynamics of a colonial species. New York: Columbia University Press.

CASAUX, R., BARRERA-ORO, E., FAVERO, M. & SILVA, P. 1998. New correction factors for the quantification of fish represented in pellets of the Imperial Cormorant *Phalacrocorax atriceps*. *Marine Ornithology* 27: 54-59.

CASAUX, R., FAVERO, M., BARRERA-ORO, E. & SILVA, P. 1995. Feeding trial on an Imperial Cormorant *Phalacrocorax atriceps*: preliminary results on fish intake and otolith digestion. *Marine Ornithology* 23: 101-106.

CASAUX, R., FAVERO, M., CORIA, N. & SILVA, P. 1997. Diet of the Imperial Cormorant *Phalacrocorax atriceps*: comparison of pellets and stomach contents. *Marine Ornithology* 25: 1-4.

COUSSEAU, M.B.; DIAZ DE ASTARLOA, J.M. & FIGUEROA, D.E. 2001. La ictiofauna de la Laguna Mar Chiquita. In: Iribarne, O. (Ed.). Reserva de Biósfera Mar Chiquita. Características Físicas, Biológicas y Ecológicas. UNESCO – Ed. Martín. pp. 187-203.

COUSSEAU, M.B. & PERROTA, R. 2000. Peces marinos de Argentina: biología, distribución y pesca (2ª edición). Mar del Plata: Instituto Nacional de Investigación y Desarrollo Pesquero.

DUFFY, D.C. & JACKSON, S. 1986. Diet studies of seabirds: a review of methods. *Colonial Waterbirds* 9: 1-17.

DUFFY, D.C. & LAURENSON, L. 1983. Pellets of Cape Cormorants as indicators of diet. *Condor* 85: 305-307.

ERWIN, R.M. 1977a. Black Skimmer breeding ecology and behavior. *Auk* 94: 709-717.

ERWIN, R.M. 1977b. Foraging and breeding adaptations to different food regimes in three seabirds: the Common Tern, *Sterna hirundo*, Royal Tern, *Sterna maxima*, and Black Skimmer, *Rynchops niger*. *Ecology* 58: 389-397.

FAVERO, M., BÓ, M.S., SILVA, M.P. & GARCÍA-MATA, C. 2000a. Food and feeding biology of the South American Tern during non-breeding season. *Waterbirds* 23: 125-129.

FAVERO, M., SILVA, M.P. & MAUCO, L. 2000b. Diet of Royal Tern (*Thalasseus maximus*) and Sandwich Tern (*Thalasseus sandvicensis*) during the austral winter in the Buenos Aires Province, Argentina. *Ornitologia Neotropical* 11: 259-262.

FAVERO, M., MARIANO-JELICICH, R., SILVA RODRÍGUEZ, M.P., BÓ, M.S. & GARCÍA-MATA, C. 2001. Food and feeding biology of Black Skimmer in Argentina: evidence supporting offshore feeding in non-breeding areas. *Waterbirds* 24: 413-418.

JOBLING, M. & BREIBY, A. 1986. The use and abuse of fish otoliths in studies of feeding habits of marine piscivores. *Sarsia* 71: 265-274.

JOHNSTONE, I., HARRIS, M., WANLESS, S. & GRAVES, J. 1990. The usefulness of pellets for assessing the diet of adult Shags *Phalacrocorax aristotelis*. *Bird Study* 37: 5-11.

LASTA, C.A. 1995. La Bahía Samborombón: zona de desove y cría de peces. Tesis doctoral. Universidad Nacional de La Plata. 304 pp.

LEAVITT, B.B. 1957. Food of the Black Skimmer (*Rynchops nigra*). *Auk* 74: 394.

RICO, R. 2000. Salinidad y distribución espacial de la ictiofauna en el estuario del Río de la Plata. Tesis de grado. Universidad Nacional de Mar del Plata.

ROSENBERG, K.V. & COOPER, R.J. 1990. Approaches to avian diet analysis. *Studies in Avian Biology* 13: 80-90.

TORNO, A.E. 1970. Descripción y comparación de los otolitos de algunas familias de peces de la plataforma Argentina. *Revista Museo Argentino de Ciencias Naturales Bernardino Rivadavia* 70: 3-20.

UNDERWOOD, A. 1997. Experiments in ecology. Their logical design and interpretation using analysis of variance. Cambridge: Cambridge University Press.

VILELA, N.M. 1988. Morfología y morfometría de los otolitos sagitta de peces del Mar Argentino. Tesis de grado. Universidad Nacional de Mar del Plata.

WHITE, D.H., MITCHEL, C.A. & SWINEFORD, D.M. 1984. Reproductive success of Black Skimmers in Texas relative to environmental pollutants. *Journal of Field Ornithology* 55: 18-30.

ZAR, J.H. 1999. Biostatistical analysis. Englewood Cliff: Prentice-Hall, Inc.

ZUSI, R.L. 1996. Family Rynchopidae (Skimmers). In: del Hoyo, J. Elliott, A. & Sargatal, J. (Eds.). Handbook of the birds of the world. Vol. 3. Hoatzin to Auks. Barcelona: Lynx Edicions. pp. 668-677.

AFRICAN PENGUINS *SPHENISCUS DEMERSUS* RECOLONISE A FORMERLY ABANDONED NESTING LOCALITY IN NAMIBIA

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SUMMARY

ROUX, J-P., KEMPER, J., BARTLETT, P.A., DYER, B.M. & DUNDEE, B.L. 2003. African Penguins *Spheniscus demersus* recolonise a formerly abandoned nesting locality in Namibia. *Marine Ornithology* 31: 203-205.

African Penguins *Spheniscus demersus* disappeared from Neglectus Islet probably between 1885 and 1952. Visiting birds were only noted rarely before the mid 1990s, but since 1995 penguin numbers on the islet have increased and breeding was first confirmed in 2001. Neglectus Islet is the only formerly abandoned nesting locality to be recolonised by African Penguins in Namibia. Although the population is still very small (estimated at around 11 breeding pairs), the re-establishment of this breeding locality is important for the conservation of the African Penguin, which is considered to be Critically Endangered in Namibia.

Keywords: African Penguin, *Spheniscus demersus*, breeding distribution, recolonisation

INTRODUCTION

Historically the African Penguin *Spheniscus demersus* probably bred at 16 localities along the Namibian coast: 14 islands and two mainland sites (Shelton *et al*. 1984, Loutit and Boyer 1985, Crawford *et al*. 1995, Whittington *et al*. 2000, Simmons & Kemper 2003, Bartlett *et al*. 2003). As the population decreased in size, a number of breeding sites became extinct (Crawford *et al*. 1995) and, in the late 1990s, penguins were breeding at only 10 localities (eight islands and two mainland sites) in Namibia (Whittington *et al*. 2000, Bartlett *et al*. 2003).

“Neglectus Islet” (26° 08.2' S, 14° 56.8' E) is a small island (unnamed on the charts) c. 80 m offshore in Hottentot Bay along the central Namib Desert coast, approximately half-way between Ichaboe and Mercury Islands. Owing to its small size (roughly 25 x 6 m), the islet has attracted little attention in the past and is poorly documented. However, it is known to be have been frequented by seabirds (African Penguins and cormorants *Phalacrocorax* sp.) since the 19th century (Eden 1846, Anon. 1885). These early descriptions led Shelton *et al*. (1984) to consider Hottentot Bay to be a former penguin breeding site abandoned for at least a century. During the first recorded visit by an ornithologist in late November 1985, Williams (1987), who named the islet, found a breeding colony of 90 nests of Bank Cormorants *P. neglectus* but no penguins (Crawford *et al*. 1995). During three of the subsequent visits, penguins were present on the islet in small numbers (four birds in November 1986, three in November 1991 and 10 in February 1994), but no signs of breeding were recorded (Crawford *et al*. 1995).

METHODS

Counts of penguins were made on five occasions from vantage points on the mainland with binoculars and spotting scopes at a distance of between 80 and 100 m. Those counts are minimum estimates, because the entire surface of the island cannot be observed from the mainland. During this study, landings on the islands was made on 28 November 1995, 10 February 2001, 15 January 2002 and 25 January 2003 and complete counts were done as well as thorough searches for nest sites and active nests. Following Kemper *et al*. (2001), active nests are defined as nests containing either eggs or chicks, and active nest sites are nests with recently added nesting material.

RESULTS AND DISCUSSION

Observations made during nine visits to Hottentot Bay between 1991 and 2003 are summarised in Table 1, together with the five previously documented visits (Crawford *et al*. 1995). Since the mid 1990s, penguins were present at Neglectus Islet during all visits, in numbers ranging from nine to 60. This contrasts with penguins being present on the islet during only three visits out of six made prior to 1995 (Table 1). One suspected nest site was recorded in 1995, and breeding had possibly occurred during that year. The first conclusive evidence of breeding was noted in February 2001 when eight active nests were found. In January 2002, nine active nest sites were found (including four active nests). Chicks, guarded and fed by adults, were also observed during two subsequent counts from the mainland (18 April and 18 November 2002). On 25 January 2003, 10 active nests, all containing eggs, were counted. An additional nest was still being constructed. Of these, seven nests and the nest site were clustered in the rubble of a collapsed structure; the other three nests were scattered amongst a colony of breeding Bank Cormorants. To date, no observations have been made between May and September. It would be useful to obtain counts during those months to establish the the seasonality of breeding on the islet.

From the data summarised in Table 1, it is clear that the numbers of African Penguins at Neglectus Islet have been increasing since 1994, and that penguins started to breed there sometime between the mid 1990s and 2001. The population linked to this colony is likely to be small at present (c. 11 breeding pairs on account of the number of nest sites found in January 2003) but is possibly still increasing. The coincidence of this recolonisation with a large population decrease at Ichaboe Island (19 km to the south) after 1995 following a Benguela Niño event (Kemper *et al*. 2001) seems to indicate that immigration of birds from Ichaboe Island, triggered by an environmental anomaly in 1994-1995, is likely to have played a role. Two banded adult penguins were observed in January 2002 but the band numbers could not be read. Another banded penguin, in late moult, was seen in January 2003. Since no penguins have been banded on Neglectus Islet, these birds must have originated from other localities.

Along the central Namibian coast, Hottentot Bay is the only sheltered bay offering safe anchorage between Lüderitz and Sandwich Harbour and has been known and used since the early days of shipping in the region. The Namibian coast has been searched intensively by sealers, whalers and subsequently guano traders since the 18th century. As was the case in many regions, early mariners regularly raided seabirds, and particularly penguin colonies to obtain fresh meat and eggs. Collections of penguins and penguin eggs have been reported many times along the Namib coast by visitors during the 18th and 19th centuries (Anon. 1845, Eden 1846, Best & Shaughnessy 1979, Kinahan 1990). A small seabird colony like that on Neglectus Islet, easily accessible in an often visited sheltered bay, was therefore particularly at risk from human depredation and disturbance. In addition, the proximity of Ichaboe Island exposed Hottentot Bay and Neglectus Islet to constant disturbance at the time of the "Ichaboe guano rush" (1843-1845), when hundreds of vessels were loading guano less than 20 km away and making use of the bay for shelter (Craig 1964). At the peak of the rush between October 1844 and January 1845, up to 460 vessels lay next to Ichaboe, frequently dragging anchor and colliding, using Hottentot Bay as temporary shelter and for repairs. In addition, at that time approximately 6000 sailors and labourers were employed in the Ichaboe guano operation and they consumed penguins and penguin eggs regularly (Anon. 1845). It is therefore likely that the bird population decreased markedly during that period. Neglectus Islet was probably also scraped for guano at that time; as the Ichaboe supply was becoming exhausted, vessels turned their attention to smaller islands (Anon. 1845, Watson 1930, Craig 1964). Yet, in June 1845, Neglectus Islet seemed to still have been frequented by seabirds since Eden (1846, p. 100) describes the islet as "a rock in Hottentot Bay, a few yards from the main land, where a small quantity of guano, and a few birds were to be seen".

Later in the 19th century penguins still remained on the islet which Captain John Spence (Anon. 1885, p. 10) describes as "a small island inside of Hottentot Bay, to which we have given the name of Hottentot Bay Island; it has a very small quantity of guano and is frequented by duikers [cormorants] and penguins." Captain Spence was at the time visiting Hottentot Bay on a yearly basis as his company, De Pass, Spence & Co., was involved in guano collection, fishing and sealing along the Namibian coast between the Orange River and Sandwich Harbour and on all the islands. Those activities included the mining of a "fossil" guano deposit (of low quality) at Hottentot Point since 1850, which yielded between 150 and 300 tons per year. A permanent establishment was maintained by that company at Hottentot Point at the time (Anon. 1885, p. 21).

The early 20th century was marked by the beginning of a Cape Rock Lobster *Jasus lalandii* fishery operating from Lüderitz. Whereas most other islands started to benefit from some protection under the authority of the Guano Islands Administration, Neglectus Islet continued to be visited without control. The fishery developed rapidly in the late 1940s and peaked in the early 1950s with approximately 14 000 tonnes of lobster caught in 1952 (Stuttaford 1994). A lobster-processing factory was built in the bay in the immediate vicinity of Neglectus Islet at that time and operated for several years. A small building, probably a pump-house now in ruin, was built on the islet itself. The construction of this building and the frequent (probably daily) visits to the islet during the lifetime of this factory was, most probably, detrimental to any remaining breeding seabird populations on Neglectus Islet. With some of the richest lobster fishing grounds being near Hottentot Bay, the fishing fleet has made extensive use of the bay to overnight and to shelter in rough weather during the fishing season to the present time (pers. obs.).

TABLE 1

Summary of African Penguin observations at Neglectus Islet for the period 1985-2002. Observations have been classified as counts from the islet itself (Is), counts from the mainland (M) or from boats around the islet (B). Counts from the mainland may not represent absolute totals because parts of the islet are not visible from the mainland. Numbers of penguins in adult plumage, immatures and total numbers of individuals (excluding chicks and fledglings) are given, as well as the numbers of active nests (AN) observed

Date	Observation	Adults	Immatures	Total	AN	Source*
29 Nov 1985	Is	0	0	0	0	1
24 Nov 1986	Is	2	2	4	0	1
6 Apr 1987	Is	0	0	0	0	1
29 Jan 1991	M	0	0	0	-	2
26 Nov 1991	B	3	0	3	0	1
Feb 1994	?	-	-	10	0	1
28 Nov 1995	Is	-	-	9	0	1
24 Nov 2000	M	16	2	18	-	2
10 Feb 2001	Is	21	3	24	8	2
15 Jan 2002	Is	33	3	36	4	2
18 Apr 2002	M	15	0	15	2	2
8 Sep 2002	M	-	-	25	-	3
18 Nov 2002	M	25	5	30	1	2
25 Jan 2003	Is	45	15	60	10	2

* Crawford *et al*. 1995 (1), this study (2), T.G. Cooper, Ministry of Environment and Tourism pers. comm. (3)

In their review, Shelton *et al*. (1984) noted that several Namibian penguin populations, particularly in the vicinity of Lüderitz, were declining or becoming extinct during the early 20th century: that of Penguin Island became extinct before 1900, Halifax Island was decreasing before 1956, North Long Island had become extinct by 1926, North Reef and Possession Island's penguin populations were already decreasing early in the century. With perhaps the exception of North Long Island, these decreases are attributable to human disturbance from the town of Lüderitz at Penguin Island, by sealers at Possession and North Reef, and by guano scrapers at Halifax Island. With intensified human presence and activity, linked to lobster fishing and processing in Hottentot Bay, it is probable that the small Neglectus Islet penguin population, if it had persisted into the 20th century, became extinct at about that time. Subsequent decreases in numbers between Lüderitz and Table Bay have been attributed to the collapse of the Sardine *Sardinops sagax* resource in Namibia and exacerbated by a shift to a system dominated by Anchovy *Engraulis capensis* in the 1970s (Crawford 1998).

Since the mid 1950s the total penguin population in Namibia has declined by 72% and is still declining (Shelton *et al*. 1984, Crawford *et al*. 1995, Kemper *et al*. 2001) and none of the other formerly occupied breeding sites has been recolonised to date. Neglectus Islet is now an established breeding locality for a Critically Endangered species in Namibia, the African Penguin (Robertson *et al*. 1998) and a globally Endangered species, the Bank Cormorant (du Toit *et al*. 2002). Therefore, despite its small size, Neglectus Islet has become important from a conservation viewpoint. It warrants careful monitoring to prevent further disturbance and legal protection together with the other Namibian seabird islands.

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REFERENCES

ANON. 1845. The African guano trade. Being an account of the trade in guano from Ichabo, and other places on the African coast. *Nautical Magazine* 11: 617-666.

ANON. 1885. Proceedings of the Angra Pequena and West Coast Claims Joint Commission. March-September 1885. Cape Town: Saul Solomon.

BARTLETT, P.A. , ROUX, J-P., JONES, R. & KEMPER, J. 2003. A new mainland breeding locality for African Penguin and Bank, Crowned and Cape Cormorants on the Namib Desert coast. *Ostrich* 74: 222-225.

BEST, P.B. & SHAUGHNESSY, P.D. 1979. An independent account of Captain Benjamin Morrell's sealing voyage to the south-west coast of Africa in the *Antarctic*, 1828/29. *Fisheries Bulletin of South Africa* 12: 1-19.

CRAIG, R. 1964. The African guano trade. *The Mariner's Mirror* 50: 25-55.

CRAWFORD, R.J.M. 1998. Responses of African Penguins to regime changes of sardine and anchovy in the Benguela system. *South African Journal of marine Science* 19: 355-364.

CRAWFORD, R.J.M., DYER, B.M. & BROWN, P.C. 1995. Absence of breeding by African Penguins at four former colonies. *South African Journal of Marine Science* 15: 269-272.

DU TOIT, M., BOERE, G.C., COOPER, J., DE VILLIERS, M.S., KEMPER, J., LENTEN, B., PETERSEN, S.L., SIMMONS, R.E., UNDERHILL, L.G., WHITTINGTON, P.A. & BYERS, O.P. (Eds.) 2002. Conservation Assessment and Management Plan for Southern African Coastal Seabirds. Cape Town: Avian Demography Unit & Apple Valley: IUCN/SSC Conservation Breeding Specialist Group.

EDEN, T.E. 1846. The search for nitre and the true nature of guano, being an account of a voyage to the south-west coast of Africa. London: Groombridge and Sons.

KEMPER, J., ROUX, J-P., BARTLETT, P.A., CHESSELET, Y.J., JAMES, J.A.C., JONES, R., WEPENER, S. & MOLLOY, F.J. 2001. Recent population trends of African Penguins *Spheniscus demersus* in Namibia. *South African Journal of marine Science* 23: 429-434.

KINAHAN, J. 1990. The impenetrable shield: HMS *Nautilus* and the Namib coast in the late eighteenth century. *Cimbebasia* 12: 23-61.

LOUTIT, R. & BOYER, D. 1985. Mainland breeding by Jackass Penguins *Spheniscus demersus* in South West Africa/Namibia. *Cormorant* 13: 27-30.

ROBERTSON, A., JARVIS, A.M., BROWN, C.J. & SIMMONS, R.E. 1998. Avian diversity and endemism in Namibia: patterns from the Southern African Bird Atlas Project. *Biodiversity and Conservation* 7: 495-511.

SHELTON, P.A., CRAWFORD, R.J.M., COOPER, J. & BROOKE, R.K. 1984. Distribution, population size and conservation of the Jackass Penguin *Spheniscus demersus*. *South African Journal of marine Science* 2: 217-257.

SIMMONS, R.E. & KEMPER, J. 2003. Cave breeding by African Penguins near the northern extreme of their range: Sylvia Hill, Namibia. *Ostrich* 74: 217-221.

STUTTAFORD, M. 1994. Recovering from the near collapse of a rich resource. Focus on fisheries and research. *Namibia Brief* 18: 12-17.

WATSON, A.C. 1930. The guano islands of southwestern Africa. *The Geographical Review* 20: 631-641.

WHITTINGTON, P., CRAWFORD, R.J.M., HUYSER, O., OSCHADLEUS, D., RANDALL, R., RYAN, P., SHANNON, L.J., WOLFAARDT, A., COOPER, J., LACY, R. & ELLIS, S. (Eds.) 2000. African Penguin Population and Habitat Viability Assessment, Final Report. Apple Valley, USA: IUCN/SSC Conservation Breeding Specialist Group.

WILLIAMS, A.J. 1987. New seabird breeding localities, and an extension of Bank Cormorant range, along the Namib Coast of southern Africa. *Cormorant* 15: 98-102.

POST-FLEDGING SURVIVAL OF MARBLED MURRELETS *BRACHYRAMPHUS MARMORATUS* ESTIMATED WITH RADIO-MARKED JUVENILES IN DESOLATION SOUND, BRITISH COLUMBIA

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SUMMARY

PARKER, N., CAM, E., LANK, D.B. & COOKE, F. 2003. Post-fledging survival of Marbled Murrelets *Brachyramphus marmoratus* estimated with radio-marked juveniles in Desolation Sound, British Columbia. *Marine Ornithology* 31: 207-212.

For many birds, juvenile survival rates are the least-known demographic component. However, such estimates are important in the construction of population projection models. Here we report the first estimates of local survival for juvenile Marbled Murrelets *Brachyramphus marmoratus*, an alcid species of conservation concern in the Pacific Northwest. We estimated the survival of 34 radio-tagged individuals to be 0.8621 (95% CI 0.7250 – 1.001) during an 80 day period post-fledging. When extrapolated over a year, under the assumption of constant survival, this translates into an annual survival rate of 0.51. In the absence of information on the influence of the transmitters on survival, our estimates were calculated with the assumption that there were no effects. Our estimates do not include fledging or early post-fledging mortality. A high proportion of radioed juveniles were censored throughout the study, and we suggest that natal dispersal may account for this. The extrapolated annual survival rate is lower than values previously used in demographic models for this species, but this work provides the first data-based evaluation of juvenile survival for the Marbled Murrelet.

Keywords: Marbled Murrelet, *Brachyramphus marmoratus*, demography, post-fledging survival, dispersal

INTRODUCTION

Post-fledging juvenile survival rates are difficult to measure, particularly for seabirds (Harris *et al*. 1994, Gaston 1997). However, several studies have highlighted the demographic importance of estimates of survival during the first year, and until first breeding, for both seabirds (e.g. Hudson 1985) and birds in general (e.g. Ganey *et al*. 1998, Hafner *et al*. 1998). Such estimates are particularly important in the construction of population projection models (e.g. Caswell 2001). Commonly used in studies with conservation implications, these models provide a standard analytical tool for estimating population growth rates as well as assessing the possible consequences of changes in various demographic parameters to these rates.

The Marbled Murrelet *Brachyramphus marmoratus* breeds in coastal old-growth forest from California to Alaska. The species is currently listed as threatened or endangered over much of its range, and the fate of these populations is linked to management decisions, which may be more effective and reliable with knowledge of the demography of the population. Despite this urgent need for a careful assessment of Marbled Murrelet population trends (Cooke 1999) estimates of several of the vital rates, including juvenile survival, are rare or missing (Ralph & Long 1995, Beissinger & Nur 1997, Boulanger *et al*. 1999). However, recent work (Cam *et al*. 2003, Bradley *et al*. 2002) has been successful in partially filling these gaps.

In the absence of studies of individually marked murrelets, estimates of annual juvenile survival for the Marbled Murrelet have previously been estimated by extrapolation from values calculated for other alcid species, and modified on the assumption that smaller alcids have lower survival rates than larger ones (see Beissinger 1995). These values have been used in population projection models to assess population growth rate (Beissinger 1995, 1997). This is the only possible approach in the absence of field data, but it is impossible to assess whether the adjustments chosen are realistic. Under any circumstances, it is best to assess population growth using data from the population(s) about which one wants to draw inferences. Parameter values from other species may differ substantially from those of the study population(s) (Cam *et al*. 2003).

Here, we report the first direct estimates of local survival rates of juvenile Marbled Murrelets, using field data from Desolation Sound, British Columbia, Canada. The Sound is a major feeding and staging area for murrelets and has been the site of a research programme investigating the demography and breeding biology of the species since 1994 (Cooke 1999, Hull *et al*. 2001, Bradley 2002, Lougheed *et al*. 2002, Cam *et al*. 2003, McFarlane-Tranquilla *et al*. 2003). Despite the longer term nature of the banding project at this site, Cam *et al*. (2003) documented that recapture rates of marked adults were extremely low, and that of juveniles marked after fledging too low to provide a meaningful estimate of local survival rate. We therefore directly investigated local juvenile survival with a telemetry study in 2001. A pilot project in and around the Sound during the 2000 season met with success in tracking radioed juveniles and suggested that post-fledging survival may be high for this area (N. Parker unpublished data). Our primary objective was to determine local survival during the early post-fledging phase of a murrelet's life.

METHODS

From 1997-2000, juvenile Marbled Murrelets were captured in Desolation Sound (centre 50° 05' N, 124° 45' W, Fig. 1), by dip-netting (Whitworth *et al*. 1997), as part of a larger banding effort for the population as a whole (see Cam *et al*. 2003). The dipnet effort typically began in mid-April of each year, and continued until mid-August (1997, 1998, 2000) or early September (1999). Juveniles were captured from the time of their first appearance on the water, usually from mid- to late June each year. Captured individuals were banded with size 3 stainless steel US Fish and Wildlife Service/Canadian Wildlife Service bands. We tallied recaptures of these birds.

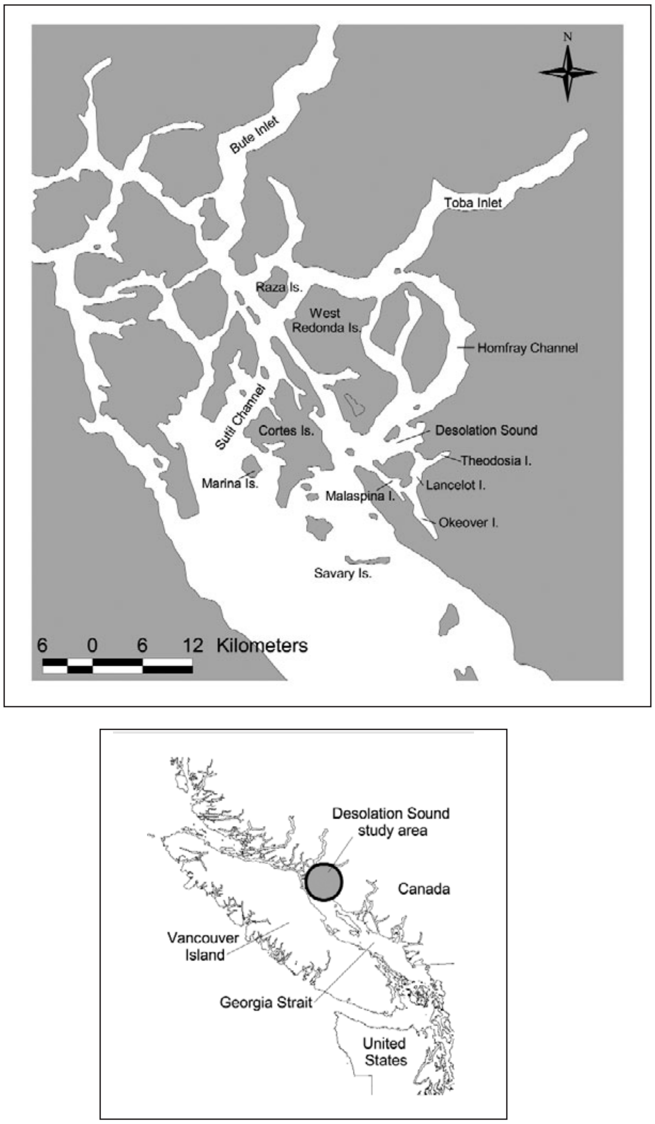

Fig. 1. Study area in Desolation Sound, British Columbia.

During the 2001 season, and based on prior knowledge of the breeding chronology of this population (McFarlane-Tranquilla *et al*., in press), captures began on June 10, 2001 before the first appearance of fledglings on the water. The first juvenile was tagged on June 25 and the last on August 11.

Captured individuals were banded with size 3 stainless steel US Fish and Wildlife Service/Canadian Wildlife Service bands as for previous years. In addition, radio transmitters (3.2g Model 386, depth ~ 4mm, diameter 3.5mm, Advanced Telemetry Systems, Inc., Isanti, Minnesota) were attached to 34 individuals following the methods of Newman *et al*. (1999) but without sutures or anaesthetic. In addition to the subcutaneous anchor, the end of the transmitter was secured to the feathers with a small amount of 3M Vetbond^{TM} Tissue Adhesive. Body coverts were then 'preened' over the unit.

Birds were tracked daily from a 5.2 m Boston Whaler, weather permitting. The study area as defined for tracking, based on the pilot project in 2000, incorporated adjacent Malaspina, Lancelot and Theodosia Inlets, and extended south to Savary Island, north to Bute Inlet, east to Homfray Channel, and west to Marina Island and the Sutil Channel (Fig. 1). The frequencies of the 34 individuals in the study were scanned from waypoints within the study area.

Although tracking began immediately following the initial captures, survival rate was estimated over eight time intervals of 10 days each, beginning July 9, 2001 and ending 26 September, 2001. We define post-fledging survival rate for the period as that estimated between these dates. The start date of 9 July 2001 corresponded to the time taken to capture a sufficient sample (n=15) to allow estimation of survival (Pollock *et al*. 1989, see also Bennetts *et al*. 1999). Tracking continued until late September. Each transmitter (Model 386) has an insured life of 80 days, and although the theoretical life expectancy (and actual, Centre for Wildlife Ecology Marbled Murrelet Project unpubl. data) is often double this, the tracking period corresponded to the insured life expectancy of the first transmitters deployed (Kenward 2001).

During each 10-day survival interval, marked individuals were located visually at least once to verify their fate. Fixed-wing tracking was initiated once we were unable to efficiently locate all juveniles from the water, within each time interval. Crews attempted to locate each individual by boat as soon as possible following flights. Extended flights were also conducted periodically in an attempt to locate censored individuals (see below) that had potentially moved beyond the range of the defined study area.

Survival estimation

We estimated the post-fledging survival rate of radio-tagged juveniles within our study area using a modification of the Kaplan-Meier method developed by Pollock *et al*. (1989). This method allows for staggered entry (i.e., not all animals are radio-tagged at the same time), and for the use of right-censored data resulting from radio failure or inability to relocate an individual once tagged (White & Garrott 1990). To avoid biasing our estimates high, we permanently censored all cases when we failed to detect a signal in a given time interval, regardless of whether the individual was subsequently detected inside the study area (see Bunck & Pollock 1993 and Bunck *et al*. 1995). We also censored individuals whose signal was detected outside the defined study area (Bunck &

Pollock 1993). Due to small sample sizes, we did not consider models allowing survival to vary with date of entry, or mass at capture (e.g. Harris & Rothery 1984, Harris *et al*. 1992, Gaston 1997).

RESULTS

Between 1997 and 2000 inclusive, a total of 106 juveniles have been banded within Desolation Sound. Of these, only two have been subsequently recaptured, both in the year following initial capture. No individuals banded as juveniles within the Sound have been detected breeding within the study area.

We estimated the survival of the 34 radiotagged juveniles during the 80 day period post-fledging to be 0.8621 (95% CI 0.7250 – 1.001, Table 2). Three juveniles were confirmed dead (Table 1). Two of these radios were tracked to trees containing eagle nests, and the third was found in an area with eagle sign. Although we cannot rule out the possibility that the carcasses were scavenged following death from other causes, Bald Eagle (*Haliaeetus leucocephalus*) predation thus seems the likely cause. Nineteen individuals were censored, of which 12 were not detected again following censoring, five were subsequently resighted at least once inside the study area, and two (Frequencies 4.111 and 5.843) were subsequently detected outside the study area. Frequency 4.111 (captured before interval 1, censored in interval 2) was detected north of Desolation Sound, on the mainland coast at the entrance to Queen Charlotte Strait (Fig. 2). In contrast Frequency 5.843 (captured in interval 2, censored in interval 4) was detected to the south, along the east coast of Vancouver Island, on three separate occasions (Fig. 2).

TABLE 1
Data from Radio-tagged juvenile Marbled Murrelets in British Columbia, Canada

Occasion	Number at risk	Number dead	Number censored	Number added
1	15	0	0	15
2	30	1	3	2
3	28	1	3	0
4	24	0	10	2
5	16	0	0	0
6	16	1	1	0
7	14	0	1	0
8	13	0	1	0

TABLE 2
Kaplan-Meier estimates of local survival in juvenile Marbled Murrelets for each time interval (July-September).

Occasion	Kaplan-Meier survival estimate	95% Confidence Interval
1	1.0000	1.0000 – 1.0000
2	0.9623	0.8990 – 1.0269
3	0.9244	0.8343 – 1.0145
4	0.9244	0.8343 – 1.0145
5	0.9244	0.8343 – 1.0145
6	0.8628	0.7250 – 1.001
7	0.8621	0.7250 – 1.001
8	0.8621	0.7250 – 1.001

DISCUSSION

Our estimate of immediate post-fledging survival is based on the first such data for both the Marbled Murrelet specifically, and for alcids in general. There was no evidence of high mortality immediately following marking, consistent with observations made during the pilot project in 2000, and also as noted by Lougheed *et al*. (2002).

We estimated a survival rate of 0.8621 for the first 80 days following capture (post-fledging survival). Based on an assumption that survival is constant over time, we extrapolated an annual survival of 0.51. The only other values for Marbled Murrelets are those of Beissinger (1995), where first year survival was assumed to be 70% that of adult survival, as suggested by Nur (1993). Using a range of survival rates for adults, Beissinger (1995) calculated a corresponding range for first year survival from 0.595-0.63. Our estimate falls below this range, but not substantially so. With regard to other alcids, most estimates of juvenile survival are reported as survival to first breeding as determined from resighting and banding recoveries in natal colonies (summaries in Hudson 1985 and Gaston and Jones 1998), which means that the survival estimate covers two or three years, and also assumes natal philopatry. However, Ydenberg (1989) presented estimates of first-year mortality using the same data from Hudson (1985). If we consider these in terms of first-year survival (i.e. 1-mortality), and use only those calculated on the assumption that mortality is highest in the first year ('method B', Ydenberg 1989), values for the atlantic alcids ranged from 0.29-0.46. In comparison, our value is higher, but not substantially so.

The following should be considered if applying our estimates more broadly. Firstly, both the 80 day and the annual extrapolations are based on data from birds carrying radio transmitters. However, Cam (unpubl. data) could not detect an influence of radios on the survival or recapture probability of adults in the Desolation Sound population, thus we have no reason to expect a large influence on juveniles. We therefore made the assumption that the transmitters did not affect individual survival.

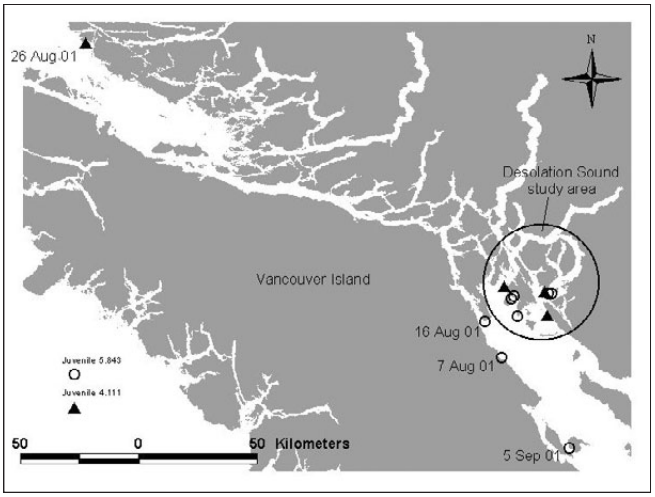

Fig. 2. Movements of two censored individuals, outside the defined study area.

Secondly, we estimated survival over a period of 80 days post-fledging, and extrapolated this, assuming constant mortality, to estimate annual survival. However, our assumption is probably unrealistic, and the resulting annual local survival estimate should be used judiciously. Juvenile survival rates for avian species may not be constant from fledging and throughout the first year. Instead periods of increased vulnerability and high mortality in that first year are commonly documented (Hudson 1985) and are usually seen as a consequence of increased risk in association with fledging and independence (Harris *et al*. 1992, Rohner & Hunter 1996), dispersal (Beaudette & Keppie 1992, Bennetts & Kitchens 1999), or the changing environmental conditions encountered during the first winter (Harris *et al*. 1994, Kersten and Brenninkmeijer 1995).

Our estimates do not account for fledging or extremely early post-fledging mortality. We used data from juveniles that successfully flew from the nest to the water and survived during a period of time of unknown length (from fledging to capture). The long flight from the nest to the ocean can be hazardous, as indicated by findings of grounded young (Carter & Sealy 1987, Rodway *et al*. 1992). The first days that follow fledging could be crucial to the survival of juvenile Marbled Murrelets as they begin to forage on their own and disperse into unfamiliar areas. Radio-equipped juveniles in this study were most frequently seen alone and in areas with fewer murrelets in general, indicating little or no post-fledging parental care (N. Parker unpubl. data, see also Kuletz & Marks 1997). This is consistent with observations for other semi-precocial Atlantic alcids (Atlantic Puffin, Black Guillemot and Dovekie, Harris & Rothery 1984, Harris & Birkhead 1985), but contrasts with a statement in Ydenberg (1989) for Marbled Murrelets. Although we attempted to catch birds as young as possible, it is likely that some birds in our sample had already survived several days on the water before capture.

Thirdly, juvenile survival has been shown to vary significantly on an annual basis for a number of seabirds (eg Harris *et al*. 1992, Harris *et al*. 1994), and for birds in general (eg Hafner *et al*. 1998, Bennetts *et al*. 1999). This parameter can also vary among regions for the same species in the same year (eg Bennetts *et al*. 1999). Further studies are needed to address the spatial and temporal variation in juvenile survival for Marbled Murrelets.

Finally, radio-telemetry studies can underestimate true survival (i.e. the quantity assessed is *local* survival), due to emigration and dispersal from a study area (Hudson 1985, Beissinger 1995), or potentially overestimate survival due to the censoring of individuals that are actually dead (e.g. Bennetts *et al*. 1999). We estimated local survival at a time when it is highly likely that juveniles were dispersing, and this may account for the large number of individuals censored. Indeed seven of the 19 censored individuals were subsequently recontacted, two of these outside the study area. Although, due to our strict criteria we censored these individuals when they were clearly alive, which could lead to the conclusion that we were in fact underestimating survival, 12 of the marked birds remained unaccounted for following censoring. Our local survival estimates are therefore based on data from individuals that remained in the study area during the tracking period.

Natal dispersal (as defined by Greenwood 1980) is common for alcids in general (Harris 1983, Hudson 1985), and may have resulted in the underestimation of juvenile survival in other radio-telemetry and capture mark-recapture studies (Hudson 1985). While very little is known of the post-breeding movements of juvenile Marbled Murrelets (Kuletz & Kendall 1998, Kuletz & Piatt 1999), we can expect dispersal to be high: the winter distribution is extensive, individuals are capable of dispersing great distances, and potential breeding habitat is extensive (Divoky & Horton 1995). The methodologies presented here did not allow a detailed investigation of natal dispersal during this study. However, the opportunistic detections of two censored individuals outside the study area do provide evidence of such dispersal.

A systematic investigation of the dispersal of Marbled Murrelets from Clayoquot Sound in 2002 documented the movement of radioed juveniles northward along the coast of Vancouver Island, and onto the mainland coast, after leaving the Sound. While this movement was initiated within days of capture for some individuals, others remained within the Sound, or near vicinity, for up to 60 days before dispersing north (Parker *et al*. MS). It is therefore not unreasonable to expect that natal dispersal confounded the estimates we present, and indeed may also account for the extremely low numbers of banded juveniles recaptured in the study area.

In studies investigating juvenile survival rates from mark-recapture and radio telemetry methods simultaneously, mark-recapture (Bennetts *et al*. 1999) or a combination of the two has been found to be preferable (Powell *et al*. 2000). As reported here the number of marked juveniles recaptured in our study area is very low. We might have expected by this time that these individuals would begin returning earlier, in greater numbers and for longer periods as they approach breeding age (e.g. Lloyd & Perrins 1977, Harris 1983, see also Gaston and Jones 1998). Despite the longer term nature of the project, we currently have little data to confidently document the age of first breeding for this species from individuals banded as juveniles. With current methodologies, and limited knowledge of natal dispersal, it may prove impossible to determine survival until first breeding in the Marbled Murrelet. Despite the limitations of our results, their value should therefore be considered in the context of current knowledge for Marbled Murrelets specifically and for seabirds in general.

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REFERENCES

BEAUDETTE, P.D. & KEPPIE, D.M. 1992. Survival of dispersing spruce grouse. *Canadian Journal of Zoology*. 70: 693-697.

BEISSINGER, S.R. 1995. Population trends of the Marbled Murrelet projected from demographic analyses. In: Ecology and Conservation of the Marbled Murrelet. Ralph, C.J., Hunt Jr., G.L., Raphael, M.G. & Piatt, J.F. (Eds.). USDA Forest Service General Technical Report PSW-GTR-152. pp. 385-393.

BEISSINGER, S.R. & NUR, N. 1997. Population trends of the Marbled Murrelet projected from demographic analysis. In: Recovery Plan for the Threatened Marbled Murrelet (*Brachyramphus marmoratus*) in Washington, Oregon, and California. Portland, Oregon. U. S. Fish and Wildlife Service.

BENNETTS, R.E., DREITZ, V.J., KITCHENS, W.M., HINES, J.E. & NICHOLS, J.D. 1999. Annual survival of snail kites in Florida: radio telemetry versus capture-resighting data. *Auk* 116(2): 435-447.

BENNETTS, R.E. & KITCHENS, W.M. 1999. With-in year survival patterns of snail kites in Florida. *Journal of Field Ornithology* 70: 268-275.

BOULANGER, J., MARTIN, K.M., KAISER, G.W. & BOYD, W.S. 1999. Evaluating uncertainty in estimating population trends of Marbled Murrelets. In: Biology and Conservation of Forest Birds. Diamond, A.W. & Nettleship, D.N. (Eds.). Society of Canadian Ornithologists Special Publication No. 1. Fredericton, New Brunswick. pp. 53-63.

BRADLEY, R.W. 2002. Breeding ecology of radio-marked Marbled Murrelets (*Brachyramphus marmoratus*) in Desolation Sound, British Columbia. Unpub. Masters Thesis. Simon Fraser University, Burnaby, BC.

BUNCK, C.M. & POLLOCK, K. H. 1993. Estimating survival of radio-tagged birds. In: Marked Individuals in the Study of Bird Population. Lebreton, J.D. & North, P. M. (Eds.). Birkhäuser Verlag Basel/Switzerland. pp. 51-63.

BUNCK, C.M., CHEN, C. & POLLOCK, K.H. 1995. Robustness of survival estimates from radio-telemetry studies with uncertain relocation of individuals. *Journal of Wildlife Management* 59:790-794.

CAM, E., LOUGHEED, L., BRADLEY, R. & COOKE, F. 2003. Demographic assessment of a Marbled Murrelet population from capture-recapture data. *Conservation Biology* 17: 1-10.

CARTER, H.R. & SEALY, S.G. 1987. Inland records of downy young and fledging Marbled Murrelets in North America. *Murrelet* 68: 58-63.

CASWELL, H. 2001. Matrix population models: Construction, analysis, and interpretation, 2nd Ed. Sinauer Associates, Inc., Sunderland, Massachusetts.

COOKE, F. 1999. Population studies of Marbled Murrelets (*Brachyramphus marmoratus*) in British Columbia. In: Biology and Conservation of Forest Birds. Diamond, A.W. & Nettleship, D.N. (Eds.). Society of Canadian Ornithologists Special Publication No. 1. Fredericton, New Brunswick. pp. 43-51.

DIVOKY, G.J. & HORTON, M. 1995. Breeding and natal dispersal, Nest Habitat Loss and Implications for Marbled Murrelet Populations. In: Ecology and Conservation of the Marbled Murrelet. Ralph, C.J., Hunt Jr., G.L., Raphael, M.G. & Piatt, J.F. (Eds.). USDA Forest Service General Technical Report PSW-GTR-152. pp. 83-88.

GANEY, J.L., BLOCK, W.M., DWYER, J. K., STROHMEYER, B.E. & JENNESS, J.S. 1998. Dispersal movements and survival rates of juvenile mexican spotted owls in Northern Arizona. *Wilson Bulletin* 110: 206-217.

GASTON, A.J. 1997. Mass and date at departure affect the survival of Ancient Murrelet *Synthliboramphus antiquus* chicks after leaving the colony. *Ibis* 139: 673-678.

GASTON, A.J. & I.L. JONES. 1998. The Auks. Oxford University Press, Oxford. pp. 349.

GREENWOOD, P.J. 1980. Mating systems, philopatry and dispersal in birds and mammals. *Animal Behaviour* 28: 1140-1162.

HAFNER, H., KAYSER, Y., BOY, V., FASOLA, M., JULLIARD, A., PRADEL, R. & CÉZILLY, F. 1998. Local survival, natal dispersal, and recruitment in Little Egrets Egretta garzetta. *Journal of Avian Biology* 29: 216-227.

HARRIS, M.P. 1983. Biology and survival of the immature Puffin *Fratercula arctica*. *Ibis* 125: 56-73.

HARRIS, M.P. & ROTHERY, P. 1984. The post-fledging survival of young Puffins *Fratercula arctica* in relation to hatching date and growth. *Ibis* 127: 243-250.

HARRIS, M.P. & BIRKHEAD, T.R. 1985. Breeding ecology of the Atlantic Alcidae. In: The Atlantic Alcidae. The evolution, distribution and biology of the Auks inhabiting the Atlantic Ocean and adjacent water area. Nettleship, D.N. & Birkhead, T.R. (Eds.). Academic Press, NY. pp. 155-204.

HARRIS, M.P., HALLEY, D. J. & WANLESS, S. 1992. The post-fledging survival of young Guillemots *Uria aalge* in relation to hatching date and growth. *Ibis* 134: 335-339.

HARRIS, M.P., BUCKLAND, S.T., RUSSELL, S.M. & WANLESS, S. 1994. Post fledging survival to breeding age of Shags *Phalacrocorax aristotelis* in relation to year, date of fledging and brood size. *Journal of Avian Biology* 25: 268-274.

HUDSON, P.J. 1985. Population parameters for the atlantic alcidae. In: The Atlantic Alcidae. The evolution, distribution and biology of the Auks inhabiting the Atlantic ocean and adjacent water area. Nettleship, D.N. & Birkhead, T.R. (Eds.). Academic Press, NY. pp. 233-261.

HULL, C.L., KAISER, G.W., LOUGHEED, C., LOUGHEED, L., BOYD, S.,& COOKE, F. 2001. Intra-specific variation in commuting distance of Marbled Murrelets (*Brachyramphus marmoratus*): ecological and energetic consequences of nesting further inland. *Auk* 118: 1036–1046.

KENWARD, R.E. 2001. A manual for wildlife radio tagging. Academic Press, NY.

KERSTEN, M. & BRENNINKMEIJER, A. 1995. Growth, fledging success and post-fledging survival of juvenile Oystercatchers *Haematopus ostralegus*. *Ibis* 137:396-404.

KULETZ, K.J. & MARKS, D. K. 1997. Post-fledging behavior of a radio-tagged juvenile Marbled Murrelet. *Journal of Field Ornithology* 68: 424-425.

KULETZ, K.J. & KENDALL, S. J. 1998. A productivity index for Marbled Murrelets in Alaska based on surveys at sea. *Journal of Wildlife Management* 62: 446-460.

KULETZ, K.J. & PIATT, J. F. 1999. Juvenile Marbled Murrelet nurseries and the productivity index. *Wilson Bulletin* 111: 257-261.

LLOYD, C.S. & PERRINS, C. M. 1977. Survival and age at first breeding in the razorbill (*Alca torda*). *Bird Banding* 48: 239-252.

LOUGHEED, C., LOUGHEED, L., COOKE, F. & BOYD, S. 2002. Local survival of adult and juvenile Marbled Murrelets and their importance for estimating reproductive success. *Condor* 104: 309-318.

MCFARLANE-TRANQUILLA, L., WILLIAMS, T. & COOKE, F. 2003. The reliability of brood patches in assessing reproductive status in the Marbled Murrelet: Words of caution. *Waterbirds* 26:108-118.

MCFARLANE-TRANQUILLA, L., WILLIAMS, T. & COOKE, F. In press. Using physiology to examine interannual variation in breeding chronology of Marbled Murrelets in Desolation Sound, B.C. *Auk*.

NEWMAN, S.H., TAKEKAWA, J.Y., WHITWORTH, D.L. & BURKETT, E. E. 1999. Subcutaneous anchor attachment increases retention of radio transmitters on Xantus' and Marbled Murrelets. Journal of Field Ornithology 70: 520-534.

NUR, N. 1993. Establishing the demographic parameters of the Marbled Murrelet. Report on file. Portland, OR: U. S. Fish and Wildlife Service.

POLLOCK, K.H., WINTERSTEIN, S.R., BUNCK, C.M. & CURTIS, P.D. 1989. Survival analysis in telemetry studies: the staggered entry design. *Journal of Wildlife Management* 53: 7-15.

POWELL, L.A., CONROY, M.J., HINES, J.E., NICHOLLS, J.D. & KREMENTZ, D.G. 2000. Simultaneous use of mark-recapture and radiotelemetry to estimate survival, movement, and capture rates. *Journal of Wildlife Management* 64: 302-313.

RALPH, C.J. & LONG, L.L. 1995. Productivity of Marbled Murrelets in California from observations of young at sea. In: Ecology and conservation of the Marbled Murrelet. Ralph, C.J., Hunt, Jr. G.L., Raphael, M.G. & Piatt, J.F. (Eds.). General Technical Report PSW-GTR-152. Albany, CA: Pacific Southwest Research Station, Forest Service, US Dept. of Agriculture. pp. 371-377

RODWAY, M.S., CARTER, H.R., SEALY, S.G. & CAMPBELL, R.W. 1992. Status of the Marbled Murrelet in British Columbia. *Proceedings of the Western Foundation of Vertebrate Zoology* 5: 17-41.

ROHNER, C. & HUNTER, D.B. 1996. First-year survival of great horned owls during a peak and decline of the snowshoe hare cycle. *Canadian Journal of Zoology* 74: 1092-1097.

WHITE, G.C. & GARROTT, R.A. 1990. Analysis of wildlife radio-tracking data. Academic Press, NY.

WHITWORTH, D.L., TAKEKAWA, J.Y., CARTER, H.R. & MCIVER, W.R. 1997. A night lighting technique for at sea capture of Xantus's Murrelets. *Colonial Waterbirds* 20: 525-531.

YDENBERG, R.C. 1989. Growth-mortality trade-offs and the evolution of juvenile life histories in the Alcidae. *Ecology* 70(5): 1494-1506.

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