

constant-sized landmark to locate a food source rely solely on visual angle for judging its distance. However, in most situations, if animals estimated distance based purely on visual angle, confusions would continuously arise. A small animal close by, which might provide a potential meal, could be confused with a larger, more distant, predator, because both would subtend the same visual angle. The ability to judge true size, taking distance into account is known as size constancy. Although size constancy has only been demonstrated in goldfish, it is hard to believe that it is not an ability common to most fish.

Polarization

Light has three variable attributes: intensity, frequency (wavelength), and polarization. While the first two of these have been extensively studied (see above), the plane of polarization, like ultraviolet sensitivity, is often forgotten, largely one assumes because humans are unable to detect it. However, there is now considerable evidence that several species of teleost display polarization sensitivity. This appears to rely on the use of double and ultraviolet-sensitive single cones within a regular photoreceptor mosaic (e.g., **Figure 13**), and fish are able to use this information for, among other things, spatial orientation and navigation.

See also

Bioluminescence. Inherent Optical Properties and Irradiance.

Further Reading

- Ali MA (1975) *Vision in Fishes*. New York: Plenum Press.
- Ali MA and Anctil M (1976) *Retinas of Fishes: An Atlas*. Berlin: Springer-Verlag.
- Archer SN, Djamgoz MBA, Loew ER, Partridge JC and Vallerga S (1999) *Adaptive Mechanisms in the Ecology of Vision*. Dordrecht: Kluwer Academic.
- Bowmaker JK (1996) The visual pigments of fish. *Progress in Retinal and Eye Research* 15(1): 1–31
- Collin SP (1997) Specialisations of the teleost visual system: adaptive diversity from shallow-water to deep-sea. *Acta Physiologica Scandinavica* 161 (supplement 638): 5–24.
- Collin SP and Marshall NJ (2000) Sensory processing of the aquatic environment. *Philosophical Transactions of the Royal Society, Biological Sciences* 355(1401): 1103–1327.
- Douglas RH and Djamgoz MBA (1990) *The Visual System of Fish*. London: Chapman and Hall.
- Douglas RH, Partridge JC and Marshall NJ (1998) The eyes of deep-sea fish I: lens pigmentation, tapeta and visual pigments. *Progress in Retinal and Eye Research* 17(4): 597–636.
- Nicol JAC (1989) *The Eyes of Fishes*. Oxford: Clarendon Press.

FISHERIES AND CLIMATE

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Every living organism responds in some way to variations in its physical environment. Fish are no exception. Variations in climatic and oceanographic conditions can lead to changes both in the geographical distribution of fish populations and in their dynamics. For obvious reasons, distributional shifts are most dramatic near environmentally controlled limits of species ranges. Perhaps the best-known example is the response to the warming of the north-east Atlantic between the 1920s and 1960s. This warming, which was related to the strengthening of the Greenland high pressure system, was marked by the appearance of subtropical species, like albacore and swordfish, at high latitudes and the return of cod and haddock to the

Barents Sea. Climatic effects on the distribution of a particular species can operate directly by altering the geographic range of physiologically tolerable conditions or indirectly by altering the distribution of prey species.

These examples illustrate occasions when the effects of climatic change can be related to presumptive causes. For most fish stocks, however, explanations of population variability in terms of climate are not so simple. The critical time in the life cycle that determines population size of fish stocks is the period from egg production, through the larval phase to accession of juveniles to the adult population. This 'recruitment' process, when numbers of offspring per parent can decrease dramatically – by factors of 10^{-3} to 10^{-5} – is the most variable but least understood part of the life cycle. Yet predicting recruitment is central to the problems of managing commercial fish stocks.

Empirical studies of the relationship between climatic and oceanographic variables and measures of

recruitment to fish stocks have a long history. A notable example is the attempt by Shepard and others to relate recruitment to 18 spring-spawning demersal stocks in the north-east Atlantic to late winter and early spring sea surface temperatures in the North Sea and west of Scotland over the period 1962–1976. Based on a principal component analysis, statistically significant correlations, both positive and negative, were found for a number of stocks.

Other efforts in the North Atlantic have attempted to focus more narrowly on the effects of specific climatic processes. Over the past century or so, the outstanding source of basin-scale variability over the North Atlantic has been the waxing and waning of the Greenland high. This is the northern pole of the North Atlantic Oscillation. This system intensified between the 1920s and 1960s and then collapsed in the 1970s. The collapse of the Greenland high was associated with the formation near Iceland of a large slug of cold, low-salinity water. This so-called Great Salinity Anomaly moved from Iceland to the west coast of Greenland to the Labrador Sea then across the Atlantic to the Faroe Shetland Channel and on to the Barents Sea. The entire circuit of the North Atlantic took 14 years. By resisting stratification, the colder waters of the Great Salinity Anomaly delayed (and possibly reduced) primary production. Cushing, Dickson, and others studied recruitment to a number of fish stocks as the Great Salinity Anomaly made its way around the North Atlantic. This analysis revealed strikingly consistent reductions in recruitment that followed the route of the Great Salinity Anomaly.

A more equivocal example from the north-east Atlantic concerned the so-called gadoid outburst that began in the 1960s and peaked in the 1970s in the North Sea. During the gadoid outburst, recruitment to demersal stocks including cod and haddock increased by a factor of four or more. Using data through 1978, Cushing related this burst of recruitment to changes in the seasonal distribution of the copepod *Calanus finmarchicus*, the primary prey of larval cod. However, when the period of analysis was extended by 10 years, the relationship vanished. Part of the problem may be that other physical or biological factors influencing recruitment were also varying during this period. For example, the beginning of the gadoid outburst coincided with, but appears not to have been caused by, the collapse of the North Sea herring and mackerel stocks. The recovery of these pelagic species, which prey on larval cod, in the 1980s may have complicated the picture. In any case, the cause of the gadoid outburst remains in some doubt.

Empirical analyses are not confined to the North Atlantic. For example, a study of recruitment to 59 regional stocks comprising 28 species in five regions in the north-east Pacific ranging from the Bering Sea to the California coast, found coherent variations in recruitment within regions with little coherence between regions. However, the effects of El Niño events were felt across the regions. The effects of El Niño on fish stocks in the eastern Pacific has received considerable attention. During an El Niño event, the eastern Pacific is flooded with warm water. The thermocline is depressed and upwelling of nutrient-rich waters is reduced or cut off. This has widespread effects on ecosystems off the west coast of South America. The collapse in the early 1970s of the Peruvian anchoveta has sometimes been attributed to the strong El Niño event in 1972. However, as this collapse appears to have begun in 1971, the role of El Niño is still unclear. The effects of El Niño are also felt along the west coast of North America. For example, a positive relationship has been found between El Niño and year class strength of Pacific mackerel, and a similar relationship was found for herring as far north as British Columbia. It is now recognized that El Niño events are one manifestation of a Pacific-wide oscillation. The effects in the eastern Pacific outlined above are mirrored by effects in the western Pacific. A striking example is the alternation between sardines and anchovies in Japanese waters. This alternation, which has been seen in other variable upwelling systems, has been attributed to differences between the two species in preferred conditions for growth, with sardines requiring warmer conditions with weak upwelling and anchovies tolerating more variability in temperature and upwelling conditions.

The empirical evidence that variations in climatic and oceanographic conditions affect recruitment is persuasive. The historical evidence, from early fisheries and from fish scales in sediment cores indicates that there was great natural variability in fish stocks before fishing effort became a dominant element in determining stock size. These data show that more than one species can display large and contemporaneous changes in abundance. However, the details of this connection for specific stocks is not always clear. Although it is unlikely that a single explanation suffices in all cases, Cushing has made a carefully reasoned argument that an important connection operates through food availability in the larval stage. This is a version of the match-mismatch hypothesis that states that successful recruitment requires that larvae be present at the time and place where food is abundant. Climatic

and oceanographic factors can intervene through effects on the magnitude and timing of primary production or on the distribution by winds and currents of larvae and their prey. A great advantage of an hypothesis of this kind is that it provides the basis for designing and interpreting empirical studies.

See also

Coral Reef and Other Tropical Fisheries. Crustacean Fisheries. Demersal Species Fisheries. Marine Fishery Resources, Global State of. Molluskan Fisheries. Open Ocean Fisheries for Deep Water Species. Open Ocean Fisheries for Large Pelagic Species. Salmon Fisheries: Atlantic. Salmon Fisheries: Pacific. Seabirds and Fisheries Interaction. Small Pelagic Species Fisheries. Southern Ocean Fisheries.

Further Reading

Baumgartner TR, Soutar A and Ferriera-Bartina V (1992) Reconstruction of the history of Pacific sardine and

northern anchovy populations over the past two millennia from sediments of the Santa Barbara basin. *California Cooperative Oceanic Fisheries Investigation* 33: 24–40.

Beamish RJ (ed.) (1995) Climatic change and northern fish populations. *Canadian Special Publication Fisheries and Aquatic Science* 121. Ottawa: National Research Council of Canada.

Cushing DH (1982) *Climate and Fisheries*. London: Academic Press.

Cushing DH (1995) *Population Production and Regulation in the Sea*. Cambridge: Cambridge University Press.

Fromentin J-M and Planque B (1996) *Calanus* and environment in the eastern North Atlantic. II. Influence of the North Atlantic Oscillation on *C. finmarchicus* and *C. helgolandicus*. *Marine Ecology Progress Series* 134: 111–118.

Jakobsson J (ed.) (1994) Cod and climate change; symposium proceedings. *ICES Marine Science Symposium*. 198. Copenhagen: International Council for the Exploration of the Sea.

Oiestad V (1994) Historic changes in cod stocks and cod fisheries: Northeast Arctic cod. *ICES Marine Science Symposium* 198: 17–30.

FISHERIES

Multispecies Dynamics

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Introduction

The abundance of marine fish populations is notoriously variable. Much attention has focused on year-to-year fluctuations in the abundance of young fish entering the fisheries (recruitment). Even larger amplitude fluctuations are apparent at timescales of tens to hundreds of years. The species in marine ecosystems have shared patterns of variability because they eat each other, compete for food and space and/or respond to shared variation in the ocean environment. This article examines temporal patterns in the abundances of commercially exploited species along with those of their predator and prey species. The dynamics of entire food webs are considered in other articles. The first part of this article illustrates some of the abundance patterns seen in marine fish communities. Next is a description of the tools available to fisheries ecologists to

explain these temporal patterns. This is followed by detailed description of alternate hypotheses and the evidence in support of these hypotheses. The article ends with a general discussion of species interactions in marine fish communities and the implications of these interactions for the conservation and management of marine fishes.

Terminology

The term fish is used broadly here to include exploited invertebrates and marine mammal species. A guild is a group of species that share life-history characteristics and feeding habits. Demersal fishes live on or near the seafloor and feed primarily on benthic animals. Pelagic fishes live in the water column and depend on the planktonic food chain. A species' trophic level is determined by its feeding habits: piscivorous fish feed on forage fish which are themselves planktivorous. The trophic interactions among species in a community are competition and predation. Decadal variations in abundance occur on timescales of 10 to 100 years.

Patterns of Variability in Exploited Fish Communities

Doctor Umberto D'Ancona collected statistics on the fisheries of the Upper Adriatic Sea before, during, and after World War I. Having noticed that the