Smith JE, Risk MJ, Schwarcz HP and McConnaughey TA (1997) Rapid climate change in the North Atlantic during the Younger Dryas recorded by deep-sea corals. *Nature* 386: 818–820.

Swart PK (1983) Carbon and oxygen isotope fractionation in scleractinian corals: a review. *Earth-Science Reviews* 19: 51–80.

Weil SM, Buddemeier RW, Smith SV and Kroopnick PM (1981) The stable isotopic composition of coral skeletons: control by environmental variables. *Geochimica et Cosmochimica Acta* 45: 1147–1153.

Wellington GM, Dunbar RB and Merlen G (1996) Calibration of stable oxygen isotope signatures in Galápagos corals. *Paleoceanography* 11: 467–480.

PATCH DYNAMICS

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Introduction

Once out of sight of land, the vastness and apparently unchanging nature of the open ocean might lead one to think that the plankton would be distributed evenly in space. In fact, this is rarely the case. Rather, planktonic organisms are generally distributed unevenly, in clumps of all shapes and sizes usually referred to as patches. As oceanographic platforms and various sensors for observing plankton have improved, we have discovered that plankton patches exist on scales of less than a meter (microscales) right up to scales of hundreds of kilometers (called the mesoscale) that are characteristic of the oceanic equivalent of storms.

We have also learned that the two main groups of plankton – phytoplankton (the microscopic plants in the ocean) and zooplankton (the small animals that usually feed on phytoplankton) – are not patchy in the same way. Rather, zooplankton seem to be organized into many more patches at smaller scales, such that their distributions sometimes approach being random. This characteristically smaller patch size of zooplankton is believed to reflect their greater ability for swimming, swarming, or other directed motions, perhaps in response to patchiness in their food sources or other environmental cues. Similarly, the spatial distribution of larval fish, which have an even greater capability for directed motion and are capable of swimming and orienting themselves in groups in response to cues in their environment, is usually even more patchy.

What does all this mean? What causes plankton patchiness? Are the causes physical, biological, or both? Are there ecological advantages or disadvantages to plankton patchiness? Does such patchiness promote or interfere with the transfer of energy and biomass from phytoplankton to zooplankton and larval fish and on to higher trophic levels?

The related issue of how small-scale physical processes influence the biology of planktonic organisms is addressed elsewhere (*see* **Small-scale Physical Processes and Plankton Biology**). There the focus is on how individual predators interact with individual prey within their physical environment. Observations of interactions between individual planktonic organisms are possible primarily in the laboratory. Here we consider patches as being comprised of groups of individual planktonic organisms: how they are actually observed by oceanographers in the ocean, how we then analyze such observations and assess their potential significance to food web dynamics.

The two approaches (patch-based versus individual-based observations) are connected as follows. Better understanding and prediction of patch dynamics and their importance to food web dynamics requires understanding of the processes by which individual organisms interact with each other and with the fluid flow. Generally, we are not yet able to make detailed observations of interactions between individual organisms in the ocean, and so we must rely on laboratory observations of individual organisms. To put these individual-based observations into an appropriate ecological context, however, it is also necessary to formulate or generalize how such individual interactions contribute to the behavior and responses at the level of a patch, which may contain millions of individuals. The other point of contact between the two approaches is to consider the case of an individual predator interacting with a patch of prey. One might reasonably ask whether there is some threshold difference in size between predator and prey at which an individual predator begins to interact with a patch of prey organisms (e.g., a gray whale feeding on a swarm of mysids) rather than with individual prey.

Because the observational technologies and analytic techniques used to study plankton patchiness are both complex and fascinating in their own right, it is wise during the discussion to follow to remain conscious of the underlying question being addressed: What are the implications of plankton patchiness to foodweb dynamics?

History

The existence of plankton patchiness was known as far back as the 1930s from observations that net tows taken simultaneously from two sides of the ship did not capture identical or often even similar collections of zooplankton. Subsequent studies and statistical analyses into the 1960s determined that this observed variability was not random but had structure, and that patches or clumps existed at sizes of less than a meter to sizes spanning hundreds of kilometers. In the 1970s continuous-flow fluorometers allowed high-resolution measurements of chlorophyll fluorescence (an indicator of the concentration of phytoplankton) continuously and simultaneously with comparable temperature observations. Similarities in the statistical distributions of fluorescence versus temperature quickly led to the realization that plankton patchiness was in large part controlled by physical turbulence. However, the fact that fluorescence distribution patterns did not exactly mimic that of the temperature field signaled that phytoplankton are not just 'passive tracers' of the flow, but that they are capable of changing their spatial distribution by growing. Comparable high-resolution observations of zooplankton distributions were more difficult to obtain, but their statistical properties differed even more from those of the temperature field, suggesting that, in addition to growth, zooplankton are also not passive tracers of the flow field because of their ability to swim and aggregate.

In the 1980s, the development of new observational techniques – moored fluorometers, instrumented multiple-net systems, multifrequency acoustics, optical plankton counters, and satellite-borne multichannel remote color sensors (to name but a few) – allowed a three-dimensional picture of the structure of patchiness and its relationship to the physical environment to emerge. In contrast, during the 1990s there was a shift toward the development of observational techniques that focused on individual organisms, usually under laboratory conditions. An exception to this trend was the development of the video plankton recorder (VPR), a towed oceanographic instrument that allowed *in situ* detection, identification, and counting of individual planktonic organisms, albeit with great manual labor in the analysis. Together with sensors of related oceanographic properties, the VPR allows construction of three-dimensional images of plankton patchiness simultaneously with a three-dimensional description of the immediate ocean environment.

In concert with the continuing emergence of an observational description of plankton patchiness in the context of the physical environment, there has also been a parallel development in our conceptual understanding of (i) the factors that create and control patchiness and (ii) the significance of patchiness to planktonic food web dynamics. Taking phytoplankton patchiness as an example, the 1970s view was that patch formation and decay was a balance between phytoplankton growth (which would act to stabilize the structure of a patch) versus small-scale turbulent mixing and diffusion (which combine to erode patch structure). The idea was that, in patches larger than some characteristic size, phytoplankton growth would win out over mixing and diffusion and the patch would be stable, but that, for patches smaller than this characteristic size, erosion by small-scale turbulent diffusion would be more efficient and the patch would be smoothed out. Around 1980, however, there was a realization that grazing by zooplankton could also affect the patchiness of phytoplankton. In addition, it was recognized that zooplankton can respond to variability in both phytoplankton abundance and physical structure by actively swimming to different positions to graze selectively in certain areas. Although recognized as an important process, the actual means by which zooplankton respond to cues in their environment and prey (both in terms of changing their distribution through swimming and by varying the intensity of their grazing) remains largely unknown.

Since the 1980s we have come to appreciate that the action of ocean currents and turbulence is much more complex than simply smoothing out smaller-scale structure through diffusive mixing. We now think more in terms of 'geostrophic turbulence', where variable currents and eddies (with structure from hundreds of meters down to submeter scales) create, distort, and evolve patches in various complex ways. Variable currents interacting with gradients in phytoplankton concentration can stretch, distort, and sharpen the boundaries of patches, sometimes creating very clear boundaries (often referred to as fronts) that separate patches from their background. Depending on the associated physical motions, these sharp frontal boundaries can increase or decrease the transfer of planktonic organisms across the front, or they can expose those predators that are capable of swimming to prey either of different concentration or of different community structure. We have also come to realize that perhaps the most important patches in terms of food web dynamics are those that tend either to recur or to persist at certain locations owing to features of coastal geometry or bottom topography interacting with the flow field. In fact, it is the very 'predictability' of these patches that makes them so important. These can be sites of enhanced tidal mixing, of increased retention of zooplankton and fish larvae due to convergent circular currents, or of increased dispersal due to the enhancement or divergence of currents. That such sites are important for the transfer of energy to higher trophic levels is evidenced by the fact that they are often sites where larger fish, as well as sea birds and marine mammals also congregate.

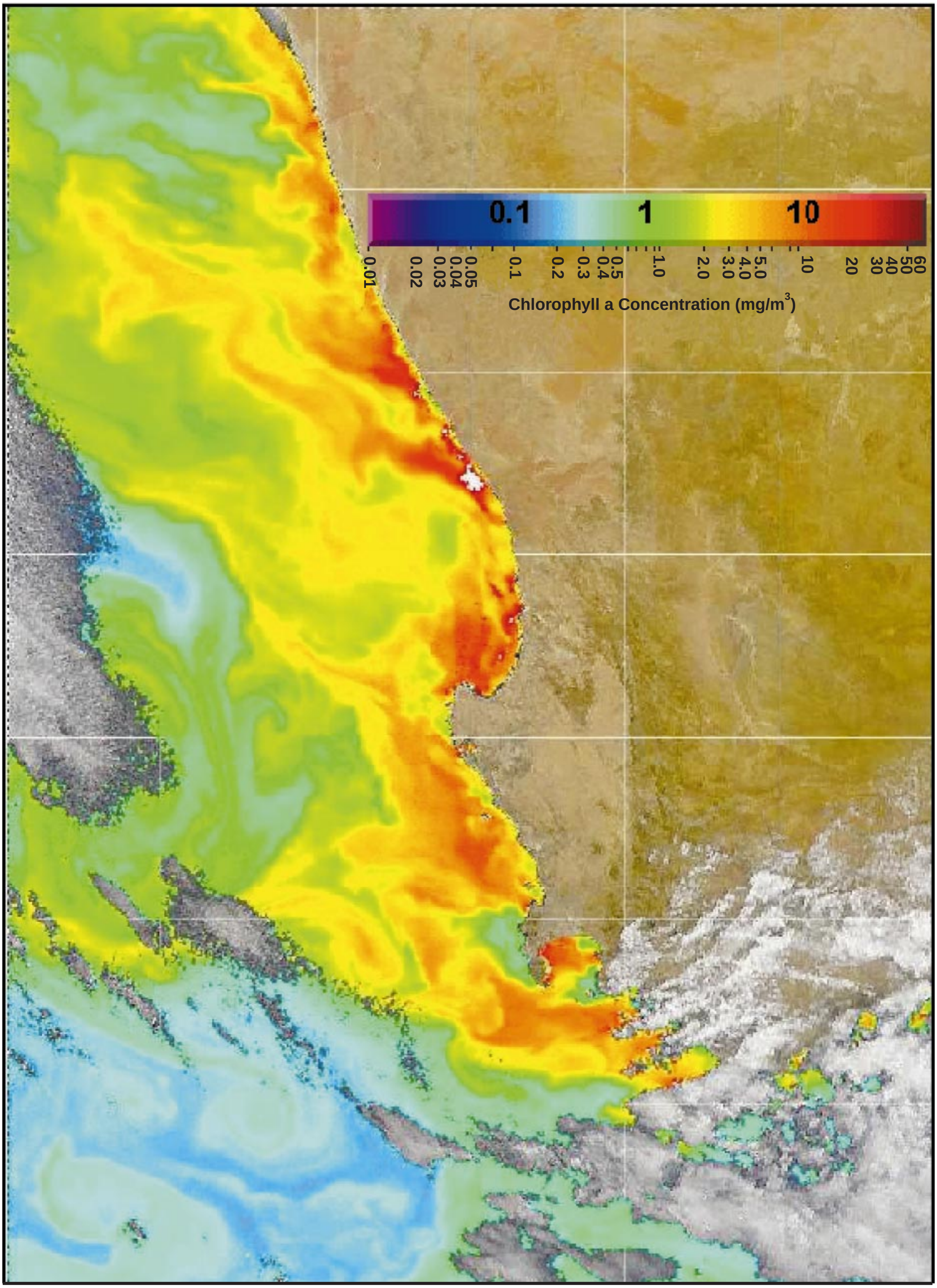
Our understanding of the importance of patchiness to food web dynamics has also evolved accordingly. Typical mean concentrations of prey organisms in the ocean, when compared with feeding studies conducted under laboratory conditions, suggest that predators generally should be starving. Other observations of predators, such as determining the contents of their guts, seem to indicate that generally they somehow get enough to eat. Initially, patchiness was evoked to solve this dilemma in the following way. Predators were thought to be capable of locating patches of their prey, then feeding to excess while in patches. Thereby, on average they were assumed to receive enough nutrition by locating patches and feeding in them. Indeed, empirical studies have demonstrated that upon encountering a patch of prey, predators that normally adopt a search pattern approximating a 'random walk' often respond by increasing their turning frequency, a behavioral adaptation apparently designed to keep the predator in the prey patch as long as possible.

Aided largely by the evolution of laboratory studies of interactions between individual predators and their prey organisms, we have further refined our understanding of how patchiness affects food web transfers by considering the role of turbulence as an active agent in feeding interactions. The basic idea is that an increase in the intensity of turbulence should increase the contact rate of predators with prey organisms (i.e., as turbulence increases, a predator should randomly encounter more prey organisms per unit time). Thus, it has been suggested that increased turbulence should allow a predator to capture more prey organisms in a given time. However, as the contact rate increases with increasing turbulence, the contact time (i.e., the length of time when the predator and prey are in close proximity to each other) decreases. Since predators need a finite time to respond to the presence of a prey item before they can capture it, we might therefore expect that as the contact time decreases the capture success of the predator will also decrease. Some model simulations suggest that, as turbulence increases, feeding success will increase, but that at some point the turbulence becomes so disruptive that feeding success starts to decrease. Whether the predator is inside or outside a patch might be expected to change the threshold at which turbulence moves from enhancing to decreasing grazing success. In addition, high turbulent intensities will also tend to spread out or disperse patches of prey.

Laboratory experiments have yet to provide definitive evaluation of these theories or hypotheses, and field observations are even more ambiguous. To add further complexity, some zooplankton are raptorial (e.g., carnivorous copepods or larval fish), seeking out and capturing individual prey organisms, while other zooplankton (notably herbivorous copepods) are filter feeders, passing water through their appendages while filtering whatever nutritional particles they can out of the water. Still others, such as jellyfish and ctenophores, are 'contact predators', which capture prey that literally bump into their tentacles. Whether these different types of predators are all affected the same way by turbulence remains to be seen. As we enter the new century, we are endeavoring to move the individual-based laboratory techniques into the field, and at the same time are developing the analytic and modeling tools to integrate our understanding of the behavior of individuals to the level of patches and populations.

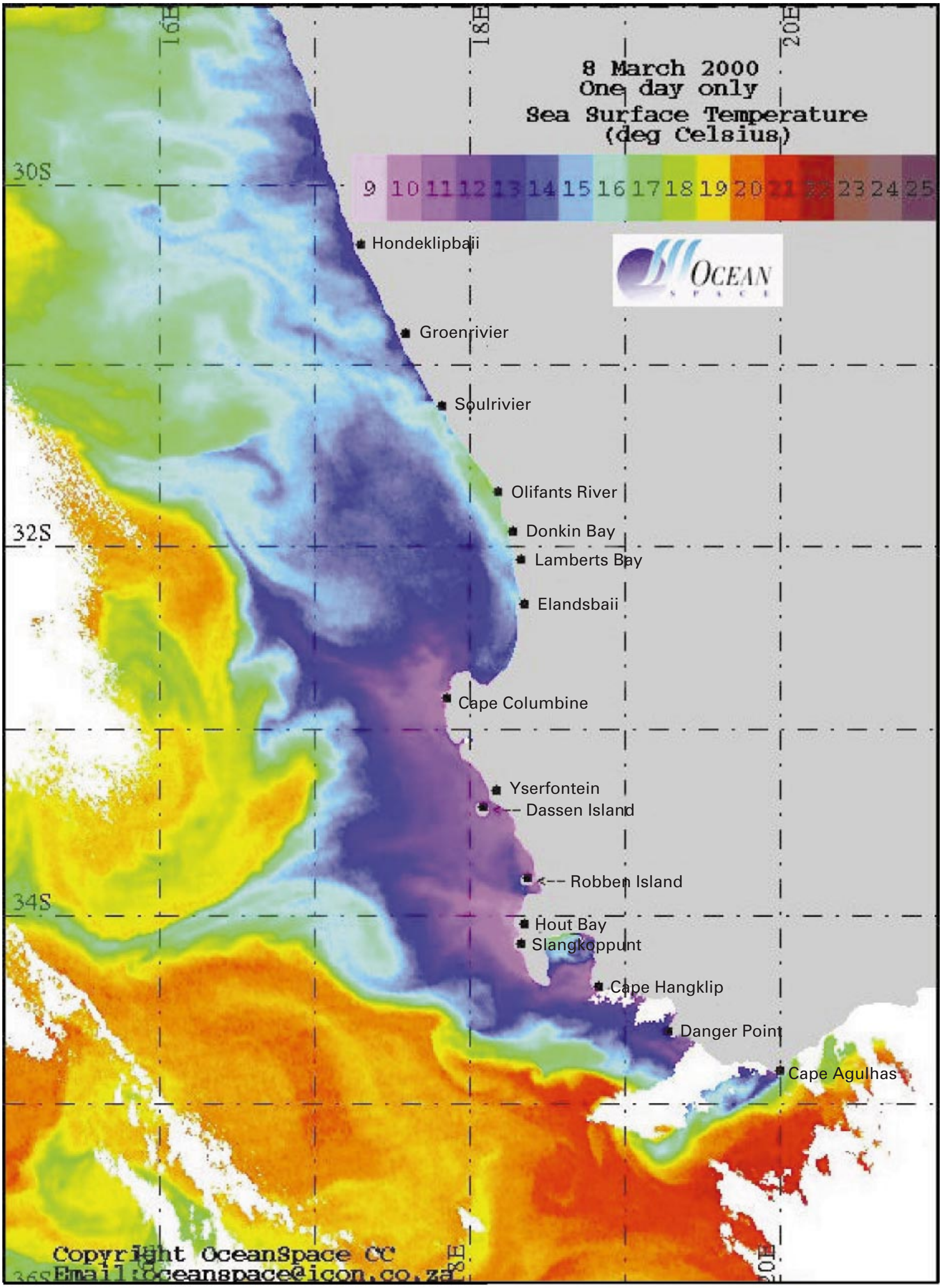
Observations and Analysis Techniques

It is not yet possible in the sea to obtain accurate 'snapshots' of the distribution of plankton over any large volume. The basic problem is that of trying to construct a synoptic (yet necessarily static) picture of the distribution of plankton, many of which display species-specific behaviors and which inhabit a three-dimensional moving fluid (which often moves in different directions at different depths). Technologies that can count individual organisms (e.g., cell cytometers for phytoplankton and video recorders for zooplankton) have both a limited range and a narrow field of view. A sufficiently dense network of sensors is rarely possible because of resource, logistical, and intercalibration limitations. A mapping strategy, whereby a grid is followed, requires a finite time for execution, during which the distribution of organisms is itself changing, blurring the 'snapshot' to an unknown degree. Within these constraints, oceanographers employ



(A)

Figure 1 (A) Derived phytoplankton pigment concentration from the SeaWiFS satellite on 8 March 2000. The image (about 800 km in the vertical dimension) shows phytoplankton patchiness (red indicates highest pigment concentration) associated with filaments of nutrient-rich upwelled waters flowing offshore from the western coast of South Africa. (B) Sea surface temperature for the same day. (Images provided by the SeaWiFS Project, NASA/Goddard Space Flight Center and ORBIMAGE, courtesy of Gene Feldman (NASA) and Scarla Weeks (OceanSpace).)



(B)

Figure 1 *Continued*

two basic types of sampling to maximize the information that they can obtain about the patchy nature of plankton distributions.

The first strategy is to tow sensors along horizontal or vertical straight lines, or along oblique 'sawtooth' paths, over a grid of transects in the horizontal plane. The second strategy involves remote sensing from satellites (**Figure 1**) or airplanes, which can give nearly 'synoptic' (snapshot) views of near surface horizontal distributions, but with little or no information on changes with depth. Such sensors include stimulated chlorophyll fluorescence, electrical conductivity, various types of acoustics, optical plankton counters, video plankton recorders, and various combinations of instrumented nets. Some of these sensors are used to count individual organisms, while others are designed to estimate plankton biomass in a given sampling volume. **Table 1** summarizes the most common sensors in terms of their spatial resolution and range, their ability to detect and count individual organisms, and the target planktonic group. Usually, oceanographers employ a combination of these sensors to obtain the best picture of the plankton distributions (**Figure 2**).

Increasingly, we want simultaneous high-resolution observations of both phytoplankton and zooplankton as well as related environmental variables (e.g., incident light, temperature, salinity, nutrients, turbulent mixing, local flow phenomena, etc.) in an attempt to identify and quantify mechanisms relating causes and consequences of patchy distributions in the planktonic ecosystem. Of course, logistic problems aside, the problem with attempting to tie all this information together is that the plankton distribution observed at some point in time may correlate better with environmental conditions at some time in the recent past (hours or days ago) rather than with the environmental conditions at the time of capture. This delay may occur because, being living organisms, plankton require time to respond to changes in their physical environment. For planktonic organisms that reproduce quickly (e.g., phytoplankton and microbes) this 'lag time' might be of the order of hours to a day. However, for organisms that take longer to grow and/or reproduce (e.g., zooplankton and larval fish) the lag time between a favorable change in the environment and a measurable response in the plankton may be of the order of days to weeks, or even longer. Thus, although we now have the technology to sample both physics and biology at very high resolutions in the ocean, we must be careful how we interpret the masses of data we collect.

Direct observations of patchiness, such as visual images from satellites and video plankton recorders, can be compelling, especially when they point to previously unknown or unexpected phenomena. But how do we proceed from 'pretty pictures' to mechanisms and then to prediction? Usually, we try to apportion the observed variability or variance into characteristic size scales: are there larger changes over kilometers or over meters? In addition, to determine interactions between different organisms or groups of organisms, or between plankton and their environment, it is necessary to perform various types of correlative analyses: are changes in phytoplankton concentrations associated mostly with changes in populations of zooplankton or with changes in temperature or nutrients? For observations obtained in a regular fashion (at regular intervals in time or space), spectrum analysis has proved to be useful, both to apportion variance according to patch size and to identify correlative structures between different variables. More recently, fractal analysis, which requires fewer assumptions regarding the 'well-behavedness' of the statistics of the observations, promises to reveal more insights into the spatial variability of plankton.

Food Web Implications

From the perspective of food web dynamics, it is interesting to consider whether plankton patchiness can be caused by predator–prey interactions. Certainly, empirical observations and some field-based work (particularly in freshwater ecosystems) have demonstrated that, under certain conditions, predation can alter plankton community structure. However, although this concept is appealing, the bulk of observational evidence in marine ecosystems strongly suggests that most plankton patchiness results from environmental factors. Examples include locally enhanced phytoplankton growth in regions of favorable light and nutrient conditions; turbulent mixing eroding patches; variable circulation patterns creating and distorting spatial structure in organism distributions; zooplankton swarming in response to environmental cues; or phytoplankton altering their buoyancy in response to variability in light, gravitational, or chemical cues. To be fair, however, it should also be noted that observations in the ocean have generally been inadequate to detect without ambiguity evidence of patchiness generated through grazing interactions. In fact, such 'top-down' regulation of planktonic concentration patterns is expected on ecological grounds. Thus, its existence should not yet be dismissed on the basis of contemporary observational capabilities.

Evidence is more clear with regard to flow patterns that can cause nutrient injection and/or the

Table 1 General properties of the most common sensors used to observe plankton patchiness. Size range of typical phytoplankton organisms is 1 μm to 20 μm; size range of typical zooplankton organisms is 1 mm to 1 cm

Sensor	*Organism*	*Range (horizontal)*	*Determine size and identity*
Fluorometer	Phytoplankton	0.1–100 km	No
Satellite color sensor	Phytoplankton	1–1000 km	No
Towed nets	Zooplankton	100 m–10 km	Yes
Optical plankton counter	Zooplankton	1 m–100 km	Size
Acoustic sounding	Zooplankton	10 m–100 km	Approximate size
Video plankton recorder	Zooplankton and phytoplankton chains	10 cm–100 km	Yes

retention or even concentration of planktonic organisms for sufficient duration that ecologically significantly enhanced feeding by predators on their prey can occur. Examples of such flow patterns are fronts, rotating rings or eddies, and regular or recurring tidal patches associated with headlands, subsurface banks, or seamounts. Persistent or regularly recurring fronts, eddies, or convergent zones may also induce behavioral adaptation in predators, especially fish populations, such that they return to sites of recurring enhanced prey. For 'passive' plankton without the capability for directed motion, it is

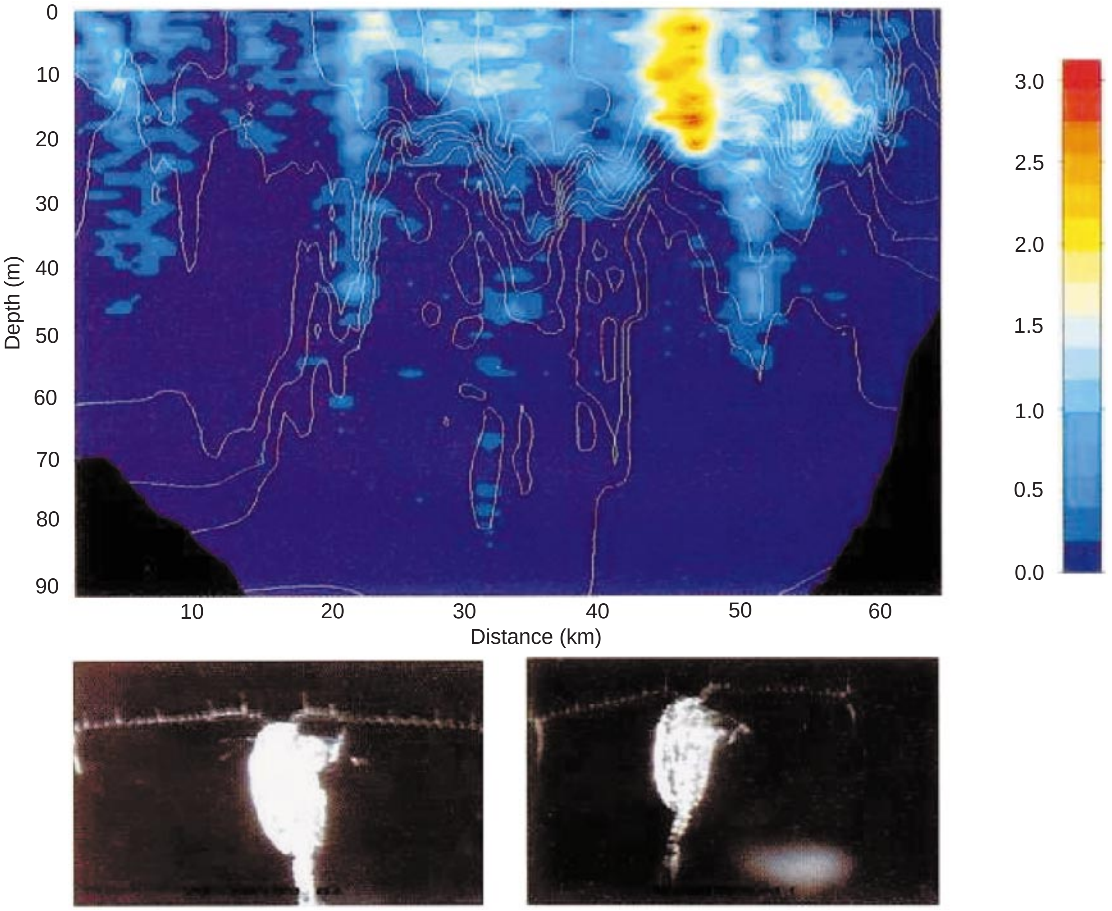


Figure 2 Distribution, abundance, and two representative images of the copepod *Calanus finmarchicus* along a transect across the Great South Channel east of Woods Hole, USA, with the video plankton recorder. Lines represent contours of constant temperature (0.5°C intervals). (From Gallager SM *et al.* (1996) High-resolution observations of plankton spatial distributions correlated with hydrography in the Great South Channel, Georges Bank. *Deep-Sea Research II* 43: 1627–1663 © 1996, with permission of Elsevier Science.

not always easy to determine whether the higher concentrations or numbers of organisms associated with these flow features result from locally enhanced growth or from concentration by convergent flow. Generally, concentration can only result when there is convergent flow and the organisms have a density different from that of the local fluid.

In recent years, our thinking has generally moved away from the concept that random encounters of patches of predators and prey result in enhanced food web transfers, and toward the concept that persistent or recurring patches (usually associated with certain flow or mixing regimes caused by particular geographical features) have the most potential to affect food web dynamics. The exception to this is the concept that turbulent motions alter the 'contact rate' between individual predator and prey organisms, an area treated in more detail in **Small-scale Physical Processes and Plankton Biology.**

What Remains 'Unknown'?

To what extent has our understanding of the importance of plankton patchiness to food web dynamics been determined by sampling inadequacies? The question can only be answered in the context of how changes in our conceptual understanding have paralleled changes in our sampling capabilities over the last several decades. As sampling capabilities have improved both under laboratory conditions and at sea, we have started to move away from considering patch–patch food web interactions. Increasingly we consider these interactions more in terms of individual predators interacting with individual prey, and determining whether 'contact rate' between predator and prey organisms is regulated mostly by the turbulent flow field or by the actions of individual predators in reponse to their sensing of prey organisms. At sea, even guided by the results of laboratory observations, we can seldom observe individual phytoplankton organisms, so conceptual models have evolved toward consideration of individual predators interacting with patches of prey. Is this the ecologically meaningful view of plankton patchiness? To resolve our conceptual uncertainties we must improve our sampling capabilities such that we can observe individual prey and predator organisms simultaneously over the dimensions of observed patches. The challenge will then be to scale up from the observations of how individual organisms interact with their environment and with other individual organisms to an understanding of how populations of organisms collectively interact with their environment and with other populations of both their predators and their prey.

See also

Bioluminescence. Fish Larvae. Moorings. Plankton. Small-scale Physical Processes and Plankton Biology.

Further Reading

Davis CS, Flierl GR, Wiebe PH and Franks PJ (1991) Micropatchiness, turbulence and recruitment in plankton. *Journal of Marine Research* 49: 109–151.

Denman KL (1994) Physical structuring and distribution of size in oceanic foodwebs. In: Giller PS, Hildrew AG and Raffaelli DG (eds) *Aquatic Ecology: Scale, Pattern and Process*. Oxford: Blackwell Scientific.

Levin SA, Powell TM and Steele JH (eds) (1993) *Patch Dynamics*, Lecture Notes in Biomathematics 96: Berlin: Springer-Verlag.

Mackas DL, Denman KL and Abbott MR (1985) Plankton patchiness: biology in the physical vernacular. *Bulletin of Marine Science* 37: 652–674.

Okubo A (1980) *Diffusion and Ecological Problems: Mathematical Models*, Berlin: Springer-Verlag.

Platt T (1972) Local phytoplankton abundance and turbulence. *Deep-Sea Research* 19: 183–188.

Platt T and Denman KL (1975) Spectral analysis in ecology. *Annual Review of Ecology and Systematics* 6: 189–210.

Powell TM and Okubo A (1994) Turbulence, diffusion and patchiness in the sea. *Philosophical Transactions of the Royal Society of London B* 343: 11–18.

Seuront L, Schmitt F, Lagadeuc Y, Schertzer D and Lovejoy S (1999). Universal multifractal analysis as a tool to characterize multiscale intermittent patterns: example of phytoplankton distribution in turbulent coastal waters. *Journal of Plankton Research* 21: 877–922.

Steele JH (ed) (1978) *Spatial Pattern in Plankton Communities*. New York: Plenum Press.

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Introduction

The pelagic organisms discussed here inhabit the epipelagic zone where biogeographic distribution of