

ACOUSTIC VISUALIZATION OF PATCH DYNAMICS IN OCEANIC ECOSYSTEMS

By Charles H. Greene, Peter H. Wiebe and Jeannette E. Zamon

Acoustic visualization combines the techniques of acoustic remote sensing and scientific data visualization.

Over the past 25 years, investigations of patch dynamics* in terrestrial and intertidal ecosystems have thoroughly revised our concepts of the processes structuring many natural communities (Levin *et al.*, 1993). Although patchiness* in the distributions of plankton has long been recognized (Steele, 1978), the patch dynamics of oceanic ecosystems have proven less amenable to direct observation and experimental investigation. Part of the problem arises from our limited ability to observe directly the processes underlying patch dynamics in the open ocean. Another part of the problem arises from the more ephemeral nature of planktonic distributions in the three-dimensional, fluid environment of the open ocean.

In recent years, satellite remote sensing has enabled us to address certain issues in oceanic patch dynamics, especially those occurring on large spatial scales (> kilometers) and those in which surface properties, such as chlorophyll fluorescence and temperature, trace important biological and physical processes at work in the ocean's interior (Shannon, 1985). Unfortunately, the resolution of satellite remote-sensing data is too coarse to address many of the issues of interest occurring on smaller scales (< kilometers). Furthermore, many of the processes relevant to patch dynamics in the ocean's interior do not express themselves in surface or near-surface properties that can be measured with sensors currently deployed on satellites. Given these limitations, alternative approaches are required for remotely sensing patch dynamics in the ocean's interior.

* Patchiness refers to the spatial heterogeneity typical of organism distributions. Patch dynamics refers to temporal changes in the patchy distributions of organisms, including the processes responsible for generating and maintaining patchiness.

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Many ocean scientists have relied on underwater acoustics to provide them with the necessary tools for remotely sensing processes at work in the ocean's interior (Clay and Medwin, 1977). Only in recent years have biological oceanographers begun to recognize the potential power of acoustics for observing the distributions of zooplankton and micronekton (see review by Greene and Wiebe, 1990; Wiebe *et al.*, 1992) and visualizing the dynamic processes at work on these distributions. Here, our intent is to illustrate through two examples how recently developed methods in acoustic visualization promise to expand greatly our understanding of patch dynamics in oceanic ecosystems.

Acoustic Visualization of Patch Dynamics: Two Examples

Acoustic visualization combines the techniques of acoustic remote sensing and scientific data visualization (Greene and Wiebe, 1994). It provides scientists with the means for interactively exploring three-dimensional data sets collected acoustically. In the examples that follow, we will describe two field investigations in which acoustic visualization has provided unique insights into problems associated with zooplankton and micronekton patch dynamics. The first example comes from an investigation designed to document the role of abrupt topography in the gap dynamics of oceanic zooplankton and micronekton. The second example comes from an investigation designed to assess the patchiness of Antarctic krill and to explore the consequences of this patchiness for predator-prey dynamics in the Southern Ocean.

The Role of Abrupt Topography in the Gap Dynamics of Oceanic Zooplankton and Micronekton

It has been hypothesized that gaps devoid of vertically migrating zooplankton and micronek-

† Gaps are a special case of patchiness, corresponding to areas (or volumes) of habitable space in which organisms are noticeably reduced in abundance relative to background levels. Gap dynamics refer to the processes associated with the formation, development, and closure of gaps.

ton form over abrupt topographic features such as submarine banks and seamounts. These gaps arise from interactions between the topography and a combination of physical and biological processes including physical advection, vertical migration behavior, and predation (Isaacs and Schwartzlose, 1965; Genin *et al.*, 1988). Specifically, the following sequence of events is hypothesized to occur. During the evening, vertically migrating zooplankton and micronekton from surrounding waters deeper than the topographic feature's summit ascend to near-surface waters. Since fewer animals ascend from waters directly overlying the feature's summit, a gap in the distribution of zooplankton and micronekton is formed. In the presence of currents, this gap may be advected partially or completely downstream during the night. The following morning, the zooplankton and micronekton descend back to deep water, except for those trapped above the summit. During the day, some of the trapped animals may escape by migrating horizontally or being swept by currents off the summit until they can descend back to deep water. Many of the remainder are consumed by predators resident to the topographic feature. In either case, the topography impedes the replenishment of deep-water zooplankton and micronekton in the area of the summit by day, thereby setting the stage for gap formation the subsequent evening.

Much of the early evidence for the gap dynamics hypothesized above was based on statistical inferences from net samples collected above and away from the summits of abrupt topography (see papers reviewed by Boehlert and Genin, 1987). During cruises in October 1990 and September 1991, we had several opportunities to document the gap dynamics of oceanic zooplankton and micronekton above Sixtymile Bank and Fieberling Guyot in the eastern Pacific (Genin *et al.*, 1994; Greene and Wiebe, 1994; Wiebe and Greene, 1994). In addition to the conventional net sampling program, we relied on acoustic remote-sensing data to visualize the daily formation, structure, and downstream advection of gaps.

The most convincing evidence for the role of abrupt topography in generating gaps in the distributions of zooplankton and micronekton comes from our investigation of Sixtymile Bank (Genin *et al.*, 1994). Sixtymile Bank is a shallow (minimum summit depth: 95 m), oval-shaped seamount occurring ~110 km southwest of San Diego, California. It is relatively small (summit dimensions: 5.0 by 3.2 km at 200 m depth) and therefore well suited to an acoustic investigation of gap dynamics, using rapid, repeated transects over the summit.

On 30 September 1991, a series of five east-west transects were conducted across the seamount from early evening until midnight (Fig. 1). The 120-kHz acoustic data from these transects re-

vealed that initial gap formation was completed by 20:17 h (Fig. 1C), after the sound-scattering layer had ascended from deep waters surrounding the seamount's summit. At its formation, the gap's horizontal extent was ~5 km, corresponding closely to the east-west dimension of the seamount's summit at the 200-m isobath. During the fourth transect (Fig. 1D), there was increasing evidence for the gap being vertically sheared and advected downstream by currents above the summit. At the completion of the final transect, near midnight (Fig. 1E), it became clear that the gap had been advected more than a kilometer eastward during the nearly 6 h of observations. The distance of the gap's downstream drift varied with depth due to vertical shear in the current velocities. Data from an acoustic doppler current profiler aboard the ship were consistent with our observations of the depth-dependent shearing of the gap (Genin *et al.*, 1994).

Single, north-south transects were conducted across Sixtymile Bank on each of three consecutive nights to document night-to-night variability in gap structure (Fig. 2). Gaps were observed to form each evening, although those observed during the first two nights were more distinctive than the one observed on the third night. This difference resulted from a change in the animal assemblage observed between the second and third nights. Net samples collected simultaneously with the acoustic data revealed that the zooplankton and micronekton shifted from an assemblage dominated by euphausiids on the first two nights to one dominated by copepods on the third night. Since euphausiids are stronger acoustic targets than copepods, the diminished intensity of the copepod-dominated, sound-scattering layer on the last night led to reduced acoustic contrast and made the gap appear less distinct (Genin *et al.*, 1994).

To explore the generality of our findings from Sixtymile Bank, we returned to an acoustic data set collected the previous October from Fieberling Guyot (Greene and Wiebe, 1994; Wiebe and Greene, 1994). Fieberling Guyot (32.5°N, 127.7°W) is a relatively isolated seamount in the eastern Pacific, occurring much further offshore than Sixtymile Bank. It is also much deeper (minimum summit depth: 435 m) than Sixtymile Bank and has a much more extensive summit area. These differences in proximity to the coast, summit depth, and summit area provided striking contrasts between the two topographic features. We felt that any evidence for comparable phenomena occurring at Fieberling Guyot would strengthen the generality of our conclusions regarding the role of abrupt topography in generating gaps in the distributions of oceanic zooplankton and micronekton.

Our primary objective in analyzing the acoustic data set from Fieberling Guyot was to look for evidence of a nighttime gap in the shallow sound-

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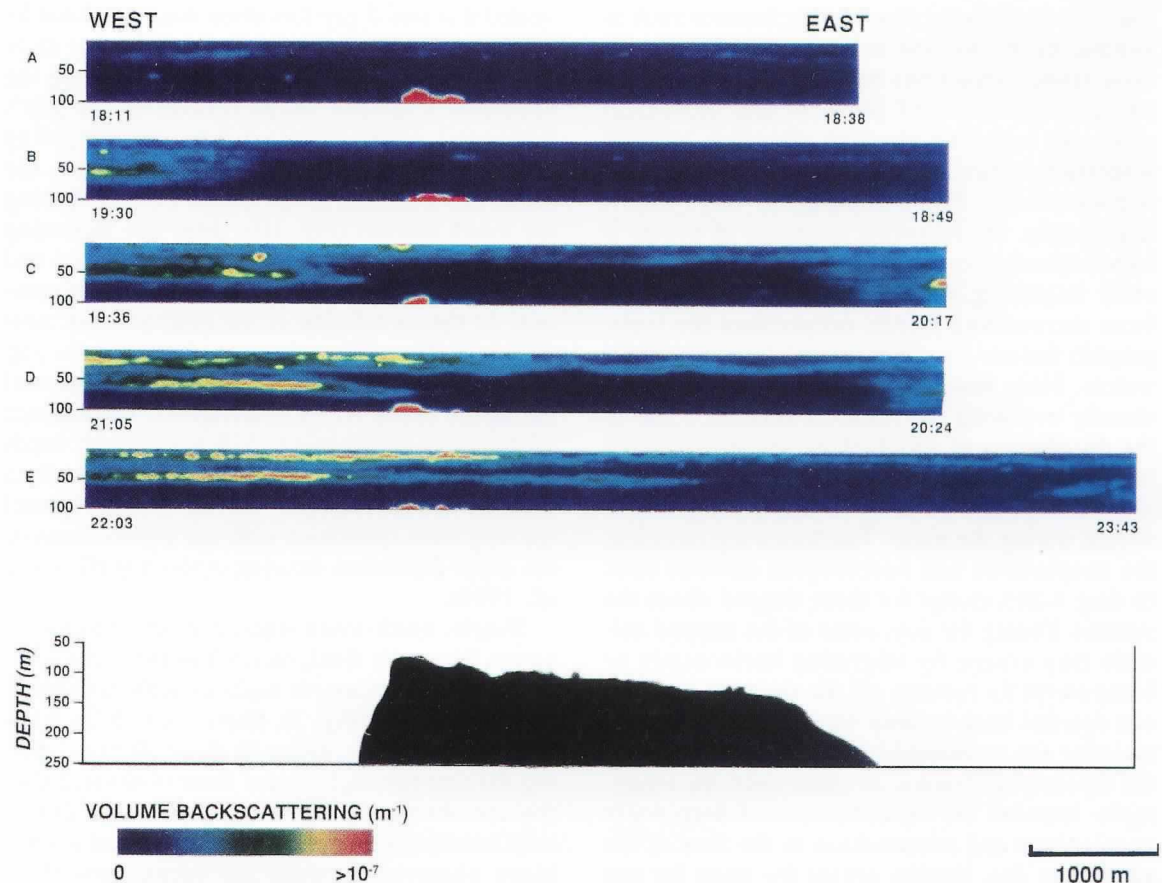


Fig. 1: Zooplankton and micronekton gap formation generated by the interaction of physical advection and animal vertical migration behavior in waters overlying abrupt topography. Time series of acoustic transect data reveals the process of gap formation over Sixtymile Bank. (A) Top panel corresponds to west-east transect prior to ascent of migrating animals. (B) Second panel corresponds to east-west transect as migrating animals reach the near-surface waters. (C and D) Third and fourth panels correspond to west-east and east-west transects after migrating animals have reached near-surface waters and gap is fully formed. (E) Bottom panel corresponds to west-east transect approximately 2 h later after gap has been sheared and advected more than a kilometer downstream. Note that local times are indicated and that the shallowest portion of the seamount's summit appears in red at the bottom of each panel (from Genin et al., 1994).

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scattering layers overlying the seamount's summit. Due to the greater depth and area of its summit, Fieberling Guyot presented a much greater logistical challenge than Sixtymile Bank. The use of a 120-kHz echo sounder limited the effective depth range of our acoustic remote sensing to the upper 120 m. The choice of 120 kHz was a compromise—lower frequencies of sound penetrate deeper in the water column, while higher frequencies are better at detecting sound-scattering layers of zooplankton. A consequence of this choice was that any evidence for the existence of a gap would have to be detectable in the upper 120 m of the water column—more than 300 m shallower than the minimum summit depth.

Due to the large areal extent of Fieberling Guyot's summit, we developed an entirely different approach to survey the waters overlying and adjacent to it. A survey pattern in the form of an eight-pointed star was designed and then followed

for two successive nights (Greene and Wiebe, 1994). This pattern ensured good areal coverage over the seamount's summit, although coverage diminished rapidly as the ship steamed away from the summit towards each point of the star. The cruise track of the survey required two nights to complete, with the ship steaming a four-pointed star on the first night and another four-pointed star, offset by 45°, on the second night. Since gaps can be observed in the surface waters only at night, acoustic data were collected between 21:00 h and 05:00 h on both nights. The timing of data collection corresponded to the nighttime period after the sound-scattering layers had completed their upward migration and before they had begun their morning descent.

The nighttime distribution of zooplankton and micronekton in the upper 120 m of the water column overlying Fieberling Guyot is visualized in Figure 3 (Greene and Wiebe, 1994). This three-di-

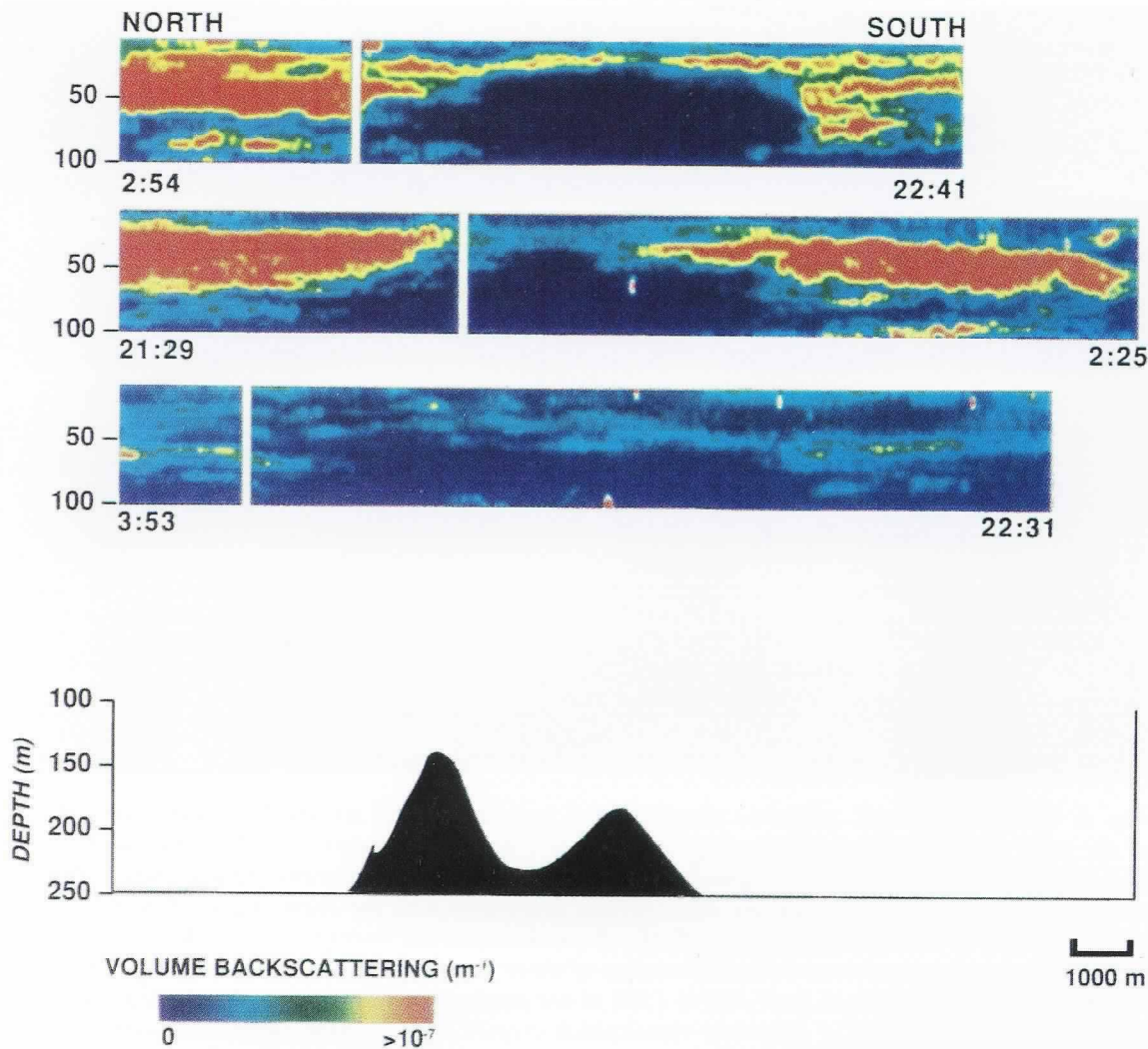


Fig. 2: Zooplankton and micronekton gaps generated by the interaction of physical advection and animal vertical migration behavior in waters overlying abrupt topography. North-south acoustic transects over Sixtymile Bank on 3 successive nights. Gaps observed on the first 2 nights were more distinctive than the one observed on the last night due to a shift in the animal assemblage's species composition. Euphausiids dominated the biomass on the first 2 nights, while copepods dominated on the last night. Since euphausiids are stronger acoustic targets than copepods, the diminished intensity of the sound-scattering layer on the last night led to reduced acoustic contrast and made the gap appear less distinct. Note that local times are indicated at the bottom of each panel (from Genin et al., 1994).

mensional, composite visualization was created from the acoustic data collected during both nights of the survey. Since the volume of water surveyed the first night would have undergone some transport prior to the second night, it may be inappropriate to interpret the figure as a synoptic visualization. Furthermore, substantial interpolation of the original acoustic data was required to generate this visualization (Greene and Wiebe, 1994). Although these issues must be recognized when interpreting the results, we believe that the composite visualization shown in Figure 3 provides us with an objective and unbiased means to look for evidence of persistent or recurring spatial structure in the data set.

During our initial inspection of the visualization, two features captured our attention immedi-

ately. The first feature is the apparent gap in the sound-scattering layer overlying Fieberling Guyot's summit. Although the presence of such a gap is what we were looking for, the lack of better survey coverage on the seamount's western flank makes the evidence less complete than we would have desired. In addition, we believe that a second observation of the phenomenon from another data set would make the case more compelling. Despite these concerns, the visualization certainly provides circumstantial evidence consistent with the gap hypothesis proposed earlier.

The second feature immediately obvious in Figure 3 is the presence of discrete sound-scattering aggregations associated with the seamount's upstream and downstream flanks. Unfortunately, the

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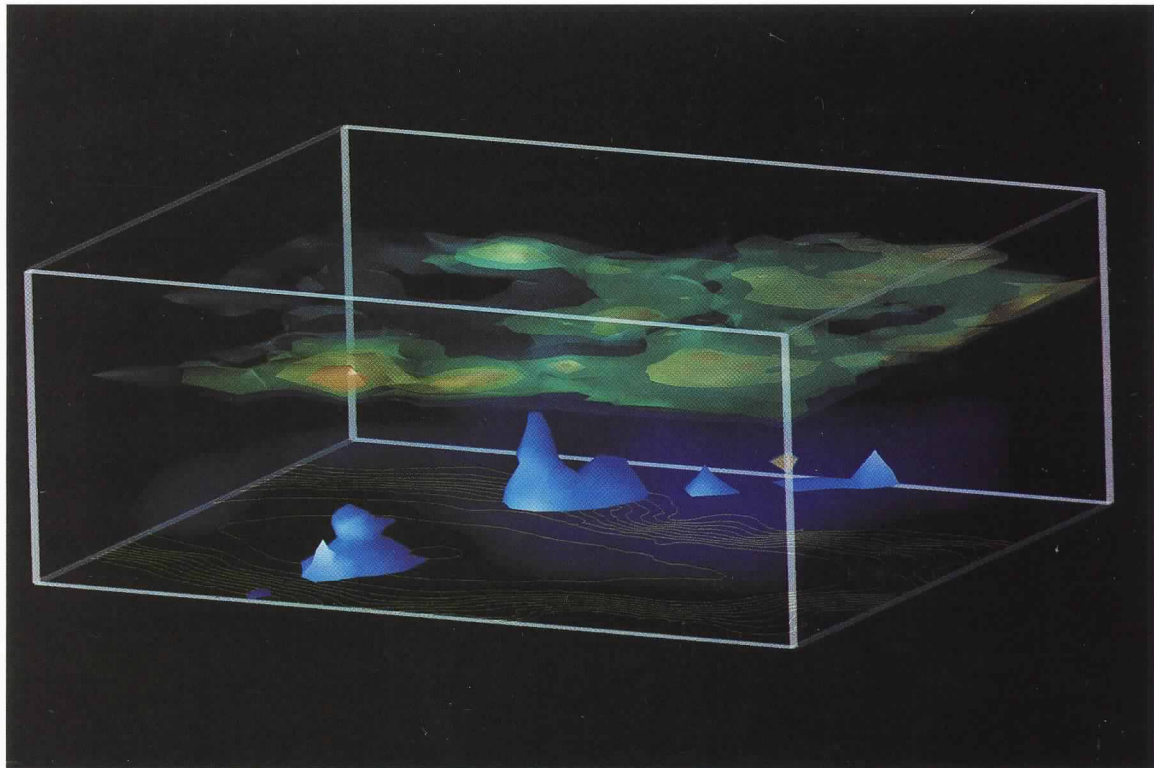


Fig. 3: Three-dimensional, nighttime distribution of zooplankton and micronekton in the upper 120 m of the water column overlying Fieberling Guyot. Note 2 prominent features in this visualization: 1) the apparent presence of a gap in the sound-scattering layer overlying the seamount's summit and 2) the presence of discrete sound-scattering aggregations associated with the seamount's upstream (into the page) and downstream (out of the page) flanks. Acoustic scattering intensity was amplified in the lower portion of the visualization to enhance imaging of these sound-scattering aggregations. Bathymetric contours of Fieberling Guyot from 500 to 1500 m are projected on the lowest horizontal plane of the visualization. This figure is a composite visualization created from acoustic survey data collected over 2 successive nights. Although data from depths greater than 120 m were collected, the low signal to noise ratio at these greater depths limited their quantitative value. Therefore, they were not included in the visualization (from Greene and Wiebe, 1994).

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full vertical extent of these aggregations could not be determined from our acoustic data. Also, we were unable to determine through conventional net sampling the identity of sound scatterers comprising these deeper, sound-scattering aggregations. The aggregations may correspond to flank-resident predators which are known from other seamounts to be demersal by day and to enter the water column at night to feed on zooplankton and micronekton (Boehlert and Genin, 1987). Other, plausible hypotheses may explain these observations, and resolution of the issue will require further investigation.

Krill Patchiness and Predator-Prey Dynamics

The Antarctic krill, *Euphausia superba*, is a keystone species in the Southern Ocean ecosystem, providing the primary source of food for a variety of top predators, including fishes, seabirds, seals, and whales (Laws, 1985). In recent years, concerns have arisen over the potential impact of localized, commercial harvesting of krill in the South Shet-

land Islands region of the Antarctic Peninsula. Given the potential for conflict between the demands of the krill fishery and efforts to conserve top predator populations in the Antarctic (May *et al.*, 1979; Nicol and de la Mare, 1993), it is essential that new methods be developed to study trophic interactions involving krill in the Southern Ocean food web. In particular, methods are needed for better assessing the availability of krill to their natural top predators as well as to the fishery.

The patchiness of krill distributions in the Southern Ocean has been demonstrated repeatedly using acoustic remote sensing (reviewed by Miller and Hampton, 1989). Rarely, however, has this work attempted to quantify patchiness on smaller spatial scales (< 100s of meters), those most relevant to foraging predators. Furthermore, prior to the field study described below [see Zamon, 1993 for a fuller description], there had never been an attempt to characterize the three-dimensional prey field of krill available to actively foraging predators.

Our field study targeted the predator-prey interaction between chinstrap penguins, *Pygoscelis antarctica*, and krill. On 13 March 1991, an acoustic survey was conducted near Elephant Island, South Shetland Islands, Antarctica (61.0°S, 54.8°W) to determine the three-dimensional distribution of krill within a volume of ocean one square nautical mile by 100 m deep. During the survey, the ship steamed a grid of six east-west and six north-south transects; each transect being one nautical mile in length. At the same time that the acoustic data were collected, penguins were counted on the surface between foraging dives. This enabled us to examine the spatial concordance between the surface distribution of foraging penguins and the depth-dependent distribution of krill.

The three-dimensional distribution of krill in the surveyed volume is visualized in Figure 4. The surface distribution of penguins is superimposed as white peaks on the surface of the volume, with the height of each peak being proportional to the number of penguins observed at a given location. Inspection of this visualization and statistical analyses of the original transect data reveal some interesting scale-dependent relationships. On the largest spatial scales investigated, penguin sightings were associated with areas in which krill were above acoustically detectable threshold values. For example, penguins were observed almost exclusively in the southern half of the surveyed volume, where krill were relatively abundant; they were rarely observed in the northern half, where krill were virtually absent. This finding was not particu-

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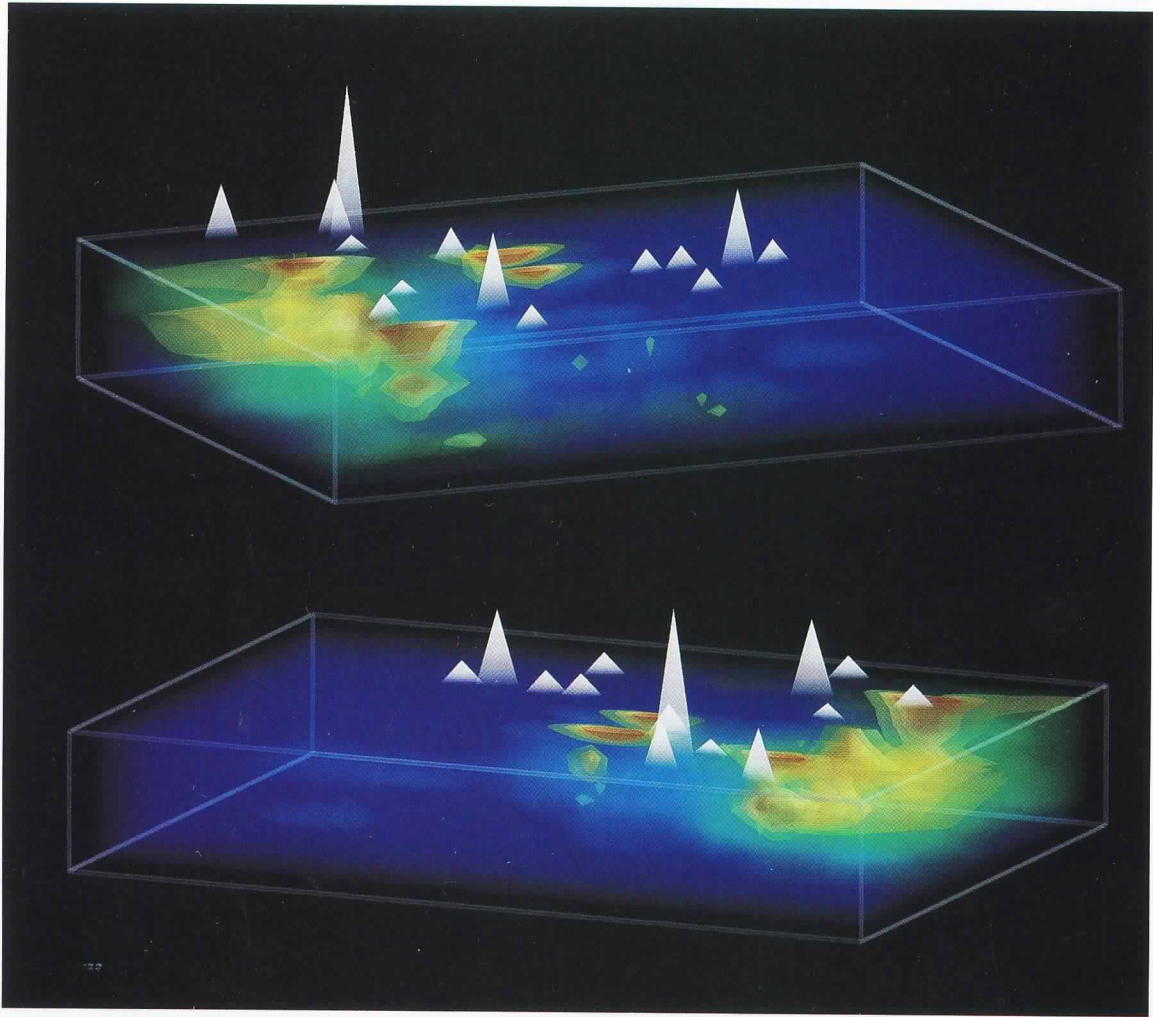


Fig. 4: Three-dimensional prey field of krill available to foraging chinstrap penguins. The rendered volume is 1 nautical mile on a side by 100 m deep. The **upper**, right-hand corner of the top panel corresponds to the northwest corner of the survey. The **lower** panel is rotated 180°. At least 6 distinct krill aggregations were present during the survey. The locations of chinstrap penguins are indicated by white peaks on the surfaces of the 2 panels. The height of a peak is proportional to the number of penguins seen at each location. The highest peak represents 20 penguins; the lowest peaks represent 2 penguins (Zamon, 1993).

larly surprising, since one might expect predators to overlap most strongly with their prey on larger spatial scales (Heinemann *et al.*, 1989; Rose and Leggett, 1990).

On smaller scales, the spatial relationships between penguin and krill distributions became more complex. Several distinct krill aggregations were detected in the southern half of the surveyed volume. Penguin surface distributions never overlapped with areas of highest krill abundance, although they did overlap with areas of moderate krill abundance. This finding could be the result of predator avoidance by the krill, inefficient searching by the penguins, or perhaps a more complex, alternative explanation. One intriguing hypothesis suggests that penguins are less efficient at hunting within krill swarms or schools and therefore may prefer to forage between such aggregations or along their edges (O'Brien, 1987). This type of behavior has been observed in other predators which feed on swarming or schooling prey (Jakobsen and Johnson, 1988).

This explanation is also consistent with another finding we had not anticipated. Despite the higher abundance of krill and their greater tendency to aggregate in the upper 30 m of the water column, the surface distribution of penguins exhibited statistically significant spatial concordance with krill distributions only between 30–50 m. One would expect that with all other things being equal, a visual, air-breathing predator would prefer to forage on shallower aggregations of prey. Although one cannot infer behavior conclusively from spatial relationships, this finding, once again, is consistent with the hypothesis that penguins may prefer to pass up opportunities to hunt where krill are most strongly aggregated. Swarming and schooling behaviors are known to be effective antipredator defenses (Hamner, 1984; O'Brien, 1987), and penguins may have adapted their foraging behavior accordingly.

Concluding Remarks

Patchiness is the rule rather than the exception in most terrestrial and oceanic ecosystems (Levin *et al.*, 1993). Due to its nearly universal occurrence, patchiness has attracted the attention of many ecologists, both landlocked and seagoing. Despite this attention, few attempts have been made, until quite recently (e.g., Steele, 1985, 1991; Levin *et al.*, 1993), to compare patchiness and patch dynamics in terrestrial and oceanic ecosystems. One explanation for the meager number of comparative studies is the common belief that these ecosystems are fundamentally different and little can be gained through comparing them (but see Steele, 1985; Steele *et al.*, 1993). Although the existence of fundamental differences between terrestrial and oceanic ecosystems cannot be denied, we believe that attempts to compare these types of ecosystems and extrapolate ecological concepts from one type to the other can yield new and important insights.

In the examples described earlier, many of the ecological issues raised are equally important in terrestrial and oceanic ecosystems. The study of gap and patch dynamics in terrestrial ecosystems has advanced rapidly in recent years (Pickett and White, 1985), due in large part to the observational and experimental tractability of these ecosystems. Although the gaps we investigated lacked the experimental tractability of their terrestrial counterparts, the conceptual framework of gap dynamics, borrowed from terrestrial ecology, encouraged us to focus our efforts on two questions of fundamental importance to both types of ecosystems: 1) *how are gaps formed*, and 2) *how do gaps close and blend in with their background*?

The answers to these questions are very different in the two types of ecosystems. As might be expected in oceanic ecosystems (Mackas *et al.*, 1985), hydrodynamic processes play a critical role in the formation and disappearance of gaps associated with abrupt topography. These gaps are formed daily from the interaction of topography with physical advection and vertical migration behavior (Genin *et al.*, 1994; Greene and Wiebe, 1994). They disappear on time scales of hours to days as a result of current shear and turbulent diffusion filling them in from the edges. In contrast, most gaps in terrestrial landscapes are formed less predictably by physical disturbance agents, such as fire and wind, or biotic agents, such as grazers and pathogens (Turner and Gardner, 1991). These gaps typically disappear over relatively longer periods of time through closure from the edges as well as recruitment and successional processes.

The lessons that we learned about gap dynamics associated with abrupt topography should not be applied indiscriminantly to other kinds of zooplankton and micronekton patch dynamics that may be occurring in the ocean. The predictability of gap formation and the rapid dynamics involved serve to make this a tractable system for study. However, it is not unreasonable to suspect that other kinds of patch dynamics in the ocean may exhibit a lesser dependence on hydrodynamic processes and/or occur over considerably longer time scales. Thus, although hydrodynamic processes often seem to dominate the patch dynamics of oceanic ecosystems, biological processes may occasionally play a role of comparable importance. Rather than emphasizing the relative roles of hydrodynamic versus biological processes, it may be more valuable to focus on their interactions (Powell, 1989). As Nihoul and Djenidi (1991) suggest, it appears to be resonance in the time scales of hydrodynamic and biological processes that determines the spatial scales and evolutionary implications of patch dynamics in oceanic ecosystems.

Our investigation of krill patchiness and predator-prey dynamics provides another perspective on the value of comparing patchiness in terrestrial

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and oceanic ecosystems. Instead of attempting to untangle the complex scale-dependent interaction of hydrodynamic and biological processes underlying krill patchiness (Levin, 1990), we chose instead to explore the consequences of this patchiness for predators foraging on krill. Although the three-dimensional fluid nature of the oceanic environment introduces some added complexity, the major ecological problems confronting predators in both types of ecosystems boil down to the same set of strategic questions.

1. If prey distributions are patchy, what is the most effective way for predators to search for prey aggregations?

2. Once prey aggregations are found, how are they evaluated and ranked by predators?

3. Once prey aggregations are evaluated and ranked, how are the highly ranked aggregations exploited most effectively by predators?

Questions like these have inspired a vast literature devoted to foraging theory (reviewed by Stephens and Krebs, 1986), a literature in which examples from oceanic ecosystems are conspicuously under-represented. Observational tractability, or the lack of it, has played perhaps the single largest role in discouraging studies of this kind in oceanic ecosystems. It is our belief that acoustic visualization has great potential for reducing some of the observational barriers currently impeding progress in such studies.

In summary, the ocean's interior will always remain a relatively dark, inhospitable environment for human exploration (Wiebe *et al.*, 1992). Nevertheless, with new methods for acoustically visualizing processes at work in the ocean's interior, ecologists can begin to gain insights into the processes associated with zooplankton and micronekton patch dynamics. These methods are particularly satisfying to use because they enable ecologists to visualize from acoustic data what they are unable to see with their own eyes directly. Perhaps as oceanic ecosystems become easier to observe and study, their similarities to as well as their differences from terrestrial ecosystems will become more apparent.

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A hypertext version of this article with animations of Figures 3 and 4 can be found on the World Wide Web via NCSA Mosaic (an Internet based global hypermedia browser). If you are not familiar with Mosaic, then you can find information about how to download it at the NCSA Mosaic anonymous FTP distribution site: <ftp.ncsa.uiuc.edu>. The URL for our article is as follows: <http://www.tc.cornell.edu:80/Research/Articles/Greene>.

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