

Interaction of ocean currents and resident micronekton at a seamount in the central North Pacific

C.D. Wilson^{a,*}, G.W. Boehlert^b

^aAlaska Fisheries Science Center, National Marine Fisheries Service, 7600 Sand Point Way NE, Seattle, WA 98115-0070, USA

^bHatfield Marine Science Center, Oregon State University, 2030 S. Marine Science Drive, Newport, OR 97365, USA

Received 18 February 2003; accepted 10 September 2003

Available online 14 May 2004

Abstract

Seamounts are often characterized by unique faunas, which may include vertically migrating micronekton species. The two dominant seamount-associated micronekton at Southeast (SE) Hancock Seamount on the northern Hawaiian Ridge are the sternophychid fish *Maurolicus muelleri* and the lophogastrid mysid *Gnathophausia longispina*. Distribution patterns for both species, based on midwater trawl and acoustic data, were compared with acoustic Doppler current profiler-measured ocean currents during four research cruises in 1987 and 1988. Populations of both species migrated above the seamount nightly. The distributions of these two species over the seamount were analyzed through acoustic surveys over the seamount flanks and summit. Differences between distributions in the first and second halves of the night were regulated by a combination of behavioral and physical processes. Ocean currents affected the localized nighttime aggregations over different regions of the summit within and between cruises. Currents over the summit had the potential to advect animals an average of 6–7 km per night during the first two cruises and about 2 km per night during the last two cruises. Net and acoustic results indicated that *G. longispina* and *M. muelleri* were displaced to the downstream side of the summit through the night, but the distances of displacement were less than would have been predicted by advection alone.

Both *G. longispina* and *M. muelleri* appeared to resist advective loss from the seamount, although the short-term distributional patterns of the two species were subject to current-mediated influences. Very few specimens were taken 5 and 10 km from the summit or above 100 m depth. Behavior patterns apparently facilitated the maintenance of these populations at this isolated seamount.

Published by Elsevier B.V.

Keywords: Seamounts; Micronekton; Acoustics; *Maurolicus*; *Gnathophausia*; Retention; Central North Pacific

1. Introduction

Seamounts are regions of complex interactions between topography and ocean currents (Roden,

1987) and are sometimes characterized by biological communities that are unusual relative to adjacent waters (Boehlert and Genin, 1987; de Forges et al., 2000; Sassa et al., 2002). Some seamounts have elevated biomass levels of zooplankton (Saltzman and Wishner, 1997), micronekton (Boehlert, 1988a; Vereshchaka, 1995), demersal and pelagic fishes (Uchida and Tagami, 1984), phytoplankton (Genin

* Corresponding author. Tel.: +1-206-526-6435; fax: +1-206-526-6723.

E-mail address: chris.wilson@noaa.gov (C.D. Wilson).

and Boehlert, 1985; Comeau et al., 1995), and anthozoan corals (Genin et al., 1986). Several seamounts support unusually large populations of fishes and invertebrates which have, in some cases, stimulated large-scale fisheries (Uchida et al., 1986), including pelagic species (Fonteneau, 1991). Despite a great deal of attention to these high biological abundances, the biophysical processes affecting populations of seamount-associated organisms are poorly understood (Boehlert and Genin, 1987) and the mechanisms supporting the unusually high biomass of a given species over a particular seamount are not well defined (Tseytlin, 1985).

Current-topography interactions likely play an important role in structuring seamount communities. On a local scale, flow disturbances may be variable and include attached eddies, internal tides, and rotary flow (Owens and Hogg, 1980; Loder et al., 1988; Noble and Mullineaux, 1989). Under certain conditions, a trapped-eddy called a Taylor column may form over the seamount through complex interactions between the seamount and impinging currents (Roden, 1987). Taylor columns have been suggested as a retention mechanism (Shomura and Barkley, 1980) and process whereby deep, nutrient-rich water is upwelled to enhance primary production (Genin and Boehlert, 1985; Bakun, 1988). Suitable time scales must exist, however, for significant biomass transfer by these kinds of mechanisms. For example, the residence time of the eddy must be long enough for the enhanced primary production to be incorporated into higher trophic levels. One of the best examples is work by Dower et al. (1992), who observed elevated levels of chlorophyll *a* above the relatively shallow summit of Cobb Seamount and suggested that the levels may have been responsible for the high biomass of benthos on that seamount.

Micronekton represent a special case of aggregation around seamounts, often including specific assemblages of animals often rare in other locations (Vereshchaka, 1995; Sassa et al., 2002). A special case is represented by the so-called “mesopelagic boundary fauna”, species that are superficially like oceanic micronekton but are resident on the slopes of islands or seamounts (Reid et al., 1991). Little is known about how these seamount-associated micronekton interact with their physical environment. Demersal seamount animals usually remain in contact with the substrate.

Micronektonic species, however, may regularly undergo diel vertical migrations to depths well above the seamount summit, and thus increase the risk of advective loss from the area. A migrating animal's response to currents may be affected by various physical and biological factors. The result may be large-scale displacement from the summit (and concomitant loss from the seamount environment), smaller displacement restricted to waters above the summit, or essentially no displacement due to behavioral station-keeping responses of the individual. Alternatively, physical mechanisms may retain these populations, as has been suggested for larval stages at certain seamounts (Mullineaux and Mills, 1997; Dower and Perry, 2001; Sponaugle et al., 2002). The responses of seamount-associated micronekton to currents are unknown, but currents may affect their distributional patterns, recruitment, and population maintenance.

Unlike strictly planktonic organisms, micronektonic and nektonic species have the potential to aggregate and exhibit directed movements (Backus et al., 1968; Pearcy et al., 1977). Mesopelagic boundary fauna at islands are proposed to make a combined horizontal and vertical migration on a diel basis, returning at dawn to the island slope (Benoit-Bird et al., 2001). Even in the open ocean, the recurrent nature of oceanic mesopelagic micronekton patches has been documented over short time scales (i.e., several diel cycles; Greenlaw and Pearcy, 1985). In addition, directed movements in response to currents have been reported for some nektonic animals. Several species of planktivorous reef fishes, for example, respond to current patterns by aggregating at the upstream side of a reef (Bray, 1981; Kingsford and MacDiarmid, 1988). Population responses to physical processes, however, are likely complex and difficult to predict; different intensities and time scales of the latter will result in different species responses and distributional patterns. Thus, a better understanding of a species' behavioral responses to physical processes, and of the resulting spatial distributions, requires investigations over a wide range of spatio-temporal scales.

At Southeast Hancock Seamount, located on the Southern Emperor–Northern Hawaiian Ridge, high densities of seamount-associated micronekton are dominated by the sternoptychid fish *Maurolicus muelleri*, and the lophogastrid mysid *Gnathophausia longispina* (Boehlert, 1988a). *M. muelleri* is a common

and widely distributed mesopelagic fish that is usually found in association with continental slope and shelf regions and mid-ocean islands and seamounts in the Atlantic and Pacific Oceans, Barents Sea, and several landlocked seas (Mukhacheva, 1981; Linkowski, 1983; Borkin and Grigorev, 1987). In some areas, such as the Benguela Current system and Norwegian fjords, population levels are remarkably high (Gjosaeter, 1981; Armstrong and Prosch, 1991). In contrast, *M. muelleri* is conspicuously absent along the west coast of North America. Very few juvenile or adult *M. muelleri* have been collected in the open ocean far from any land masses (Boehlert et al., 1994). The bathymetric range of juveniles and adults varies from near-surface waters to about 500 m in most areas because of their diel vertical movements to shallower depths at night (Okiyama, 1971; Clarke, 1982; Kalinowski and Linkowski, 1983). Studies from some areas, however, have reported daytime depths to within 50 to 120 m of the ocean surface suggesting a high degree of plasticity in distribution that may be dependent on the local environment (Dalpadado and Gjosaeter, 1987a; Armstrong and Prosch, 1991; Torgersen et al., 1997). Historical information on *G. longispina* is rare because of the paucity of specimens (summarized in Clarke, 1962). The species' distribution appears limited to areas in the Pacific Ocean within proximity to land (Clarke, 1962; Reid et al., 1991), as far north as Japan (31°40'N), and south (7°36'S) and west (117°29'E) to the various landlocked seas in the East Indies, and east to Palmyra Island (162°06'W). The highest observed abundances have been at Southeast (SE) Hancock Seamount (Wilson and Boehlert, 1993).

The effect of currents on the small-scale distributional patterns of these two dominant species is unknown. In the absence of certain behavioral responses, large numbers of these species may be lost from the seamount when currents exceed some minimum threshold. Alternatively, the species may concentrate over upstream or downstream summit regions or may exhibit no distributional relationship at all with current patterns over the summit. Vertical distributional patterns may also alter the degree to which either species is exposed to currents above the summit. In the present study, we describe the small-scale distributional patterns of *M. muelleri* and *G. longispina* at SE Hancock Seamount over short time

scales (hours to days) and relate these patterns to the ocean currents over the summit during the biological sampling.

2. Methods

All work was conducted over SE Hancock Seamount (29°48'N, 179°04'E), which is located on the Hawaiian Ridge in the central North Pacific (Fig. 1). The flat-topped summit of SE Hancock Seamount is about 2.4 km in diameter (4.5 km²) at a depth of approximately 260 m. It is the highest of several peaks collectively called Hancock Seamount. Bottom depths reach 5200 m approximately 22 km from the summit to produce an average slope along the flanks of 22% (Brainard, 1986).

Biological and physical oceanographic data from SE Hancock Seamount were collected during four cruises aboard the NOAA ship *Townsend Cromwell* in 1987 and 1988. Cruises generally lasted about two weeks each and took place during summer 1987 (8–25 August), winter 1988 (12–30 January), summer 1988 (13–26 July and 19–21 August), and fall 1988 (26 October–8 November).

2.1. Physical data collection and analyses

A complete presentation of the methods and description of the current patterns over the summit of SE Hancock Seamount are presented in Wilson (1992) and will be covered only briefly here. Data from expendable bathythermographs (XBTs) were used to describe the vertical temperature structure of the upper water column for each cruise. Estimates of current velocities over the seamount were made with data from a 150 kHz shipboard acoustic Doppler current profiler (ADCP), which was bottom tracking while over the summit.

The ADCP data were initially sampled over 45-s intervals during the summer 1987 and winter 1988 cruises, and over 1-min intervals during the summer and fall 1988 cruises. An 8 m pulse length and bin width were used on all cruises except the second half of the summer 1987 cruise when mostly 4 m values were used. All data were later averaged over 5 to 20 min time intervals and vertically into seven 24 m depth strata from 42 to 210 m. Above 40 m,

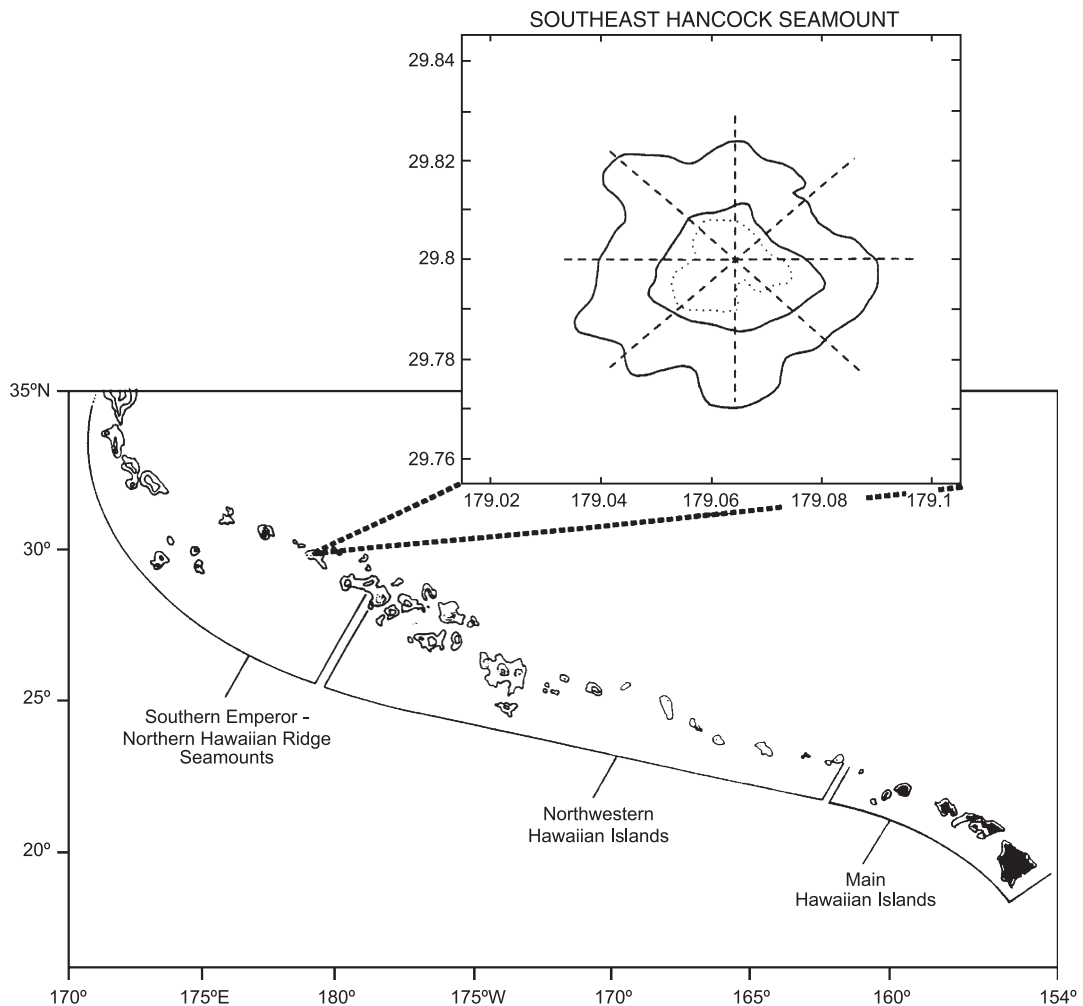


Fig. 1. Location of Southeast Hancock Seamount. Summit transects are dashed lines. Summit bottom contours shown are 700 and 300 m (solid) and 260 m (dashed).

the velocity estimates were unreliable (Wilson and Firing, 1992). Currents in the 40–210 m depth range were nearly uniform in the horizontal over the summit (Wilson, 1992). Thus, all ADCP data collected over the summit were treated without regard to the particular region in which they were collected.

To determine the potential net displacement of water and particles above the summit, progressive vector diagrams were constructed with ADCP data from the four deepest strata (114–138, 138–162, 162–186, 186–210 m), the depth zone with greatest seamount-associated acoustic backscattering (see

Results). Water velocities were integrated with respect to time for the entire night period, which was considered to extend from about 1 h after sunset until 1 h before sunrise. On a few nights when biological sampling was conducted and no ADCP data were available (that is, the ADCP was beyond the range for bottom tracking), progressive vector plots were generated from velocities predicted with a tidal model that described the currents over the summit (Wilson, 1992). Estimates of mean speed are based on trajectory distances rather than net displacements. The difference is insignificant in many cases but was done to provide the best estimate of the current speed

that an animal would experience if it maintained its horizontal position. Estimates of current velocity are averaged for depths of 114–210 m unless stated otherwise. The current velocity estimates did not appear biased by coherent, directed movements of the seamount-associated scattering except those in the deepest depth stratum during very short periods of time around sunrise (Wilson and Firing, 1992). Estimates of ADCP current velocities and densities of *M. muelleri* and *G. longispina* were not compared within about 1 h of sunrise, so the current velocities were assumed to be unbiased from horizontal animal movements.

2.2. Biological data collection and analyses

2.2.1. Trawl data

Samples were collected with a 1.8 m Isaacs–Kidd midwater trawl (IKMT) with a 2.9 m² mouth opening and a 3 mm mesh net body. A 3 mm mesh cod end was used during the spring and summer 1987 cruises and a 0.505 mm mesh cod end was used on subsequent cruises. Average ship speed for the IKMT tows was 1–2 m s⁻¹. Net sampling occurred at night. Tows were generally 1 h long. The volume of water filtered during each tow was determined with a calibrated General Oceanics Model 2030R flowmeter. A net depth profile during each tow was determined with a Benthos time–depth recorder attached to the IKMT depressor.

Horizontal IKMT tows were made across the summit at nominal depths of 200, 150, 100, and 50 m to determine the vertical distribution of *M. muelleri* and *G. longispina*. Large- and small-scale horizontal distributional patterns of *M. muelleri* and *G. longispina* around the seamount were also investigated. Large-scale distributional patterns were described by oblique IKMT tows to a nominal depth of 275 m at four stations located 5 and 10 km, up- and downstream of the summit (hereafter called off-summit zones). Small-scale horizontal distributional patterns around the summit for a given night were determined by conducting paired oblique IKMT tows to a nominal depth of 250 m within about 2 km immediately up- or downstream of the summit edge (hereafter called summit–flank zones). Although the summit area was divided into three equal parts on the first cruise, a downstream and two

other summit–flank zones, time constraints required modification of this design into the up- and downstream summit–flank zones used on subsequent cruises. Bottom depths on summit–flank tows were generally greater than 350 m. Density estimates between summit–flank zones were compared with a Wilcoxon paired-sample test (Zar, 1984). On nights when an unequal number of tows were conducted in the summit–flank zones, the median catch within each treatment zone was used in the statistical test.

The catch from each tow was immediately removed from the net and fixed in a ca. 4% buffered formaldehyde and seawater solution for later processing in the laboratory. In the laboratory, specimens of *M. muelleri* and *G. longispina* were removed from the samples and counted. All abundance estimates were adjusted to represent the number of individuals per 10,000 m³ of water filtered.

2.2.2. Acoustic data

Acoustic data were collected to describe the sound scattering layer (SSL) at SE Hancock Seamount. These data could be collected more quickly and provided a higher degree of spatial resolution than net data, whereas the latter provided species-specific estimates of abundance and distribution.

Observations of acoustic scattering were made with a 38 kHz Simrad echo sounder (Model EQ-38) operating with a nominal 0.5 Hz ping rate, 0.3 ms pulse length, and 500 W power output. A Raytheon-JRC chromoscope was configured to display the signal of the echosounder by assigning the echo voltage into one of eight bins on the basis of signal strength. Each bin was represented by a unique color displayed on the video monitor as a function of depth and ship position. The composite chromoscope screen images were photographed (35 mm color slides) for later data analysis. System calibration and the echo integration analysis (estimation of relative acoustic density of the scattering layer) are described in detail in Wilson and Boehlert (1990) and briefly below.

Absolute estimates of abundance in terms of numbers of individuals per unit volume were not generated with the acoustics data for *M. muelleri* and *G. longispina* for several reasons. It was not possible to discriminate between these two species acousti-

cally, although the trawl data provided information to confirm that much of the backscattering was attributed to them (see below). In addition, the generation of absolute abundance estimates for each species by proportional allocation of the total backscattering based on the species composition of the trawl data (MacLennan and Simmonds, 1992) was considered inappropriate. This method requires target strength (TS) estimates for each species. No TS estimates exist for either species at 38 kHz although preliminary estimates are available at 88 kHz for *M. muelleri* (Hamano and Uchida, 1992) and 200 kHz for *G. longispina* (Benoit-Bird and Au, 2001). However, target strength estimates are frequency dependent and the relationship between the two is often unpredictable (Foote et al., 1990; MacLennan and Simmonds, 1992). Thus, the proportional allocation approach was considered overly complex given the current level of understanding of TS for these two species. Instead, relative acoustic density estimates (RAD) were simply generated from the echo voltages because fundamentally, the biomass of sound scatterers is proportional to the echo voltage squared (Johannesson and Mitson, 1983; Wilson and Boehlert, 1990). Because the TS of *M. muelleri* likely exceeds that of *G. longispina* based on differences in anatomical and material properties (e.g., swim bladder), large changes in the species composition could potentially confound the interpretation of trends based solely on RAD estimates.

Acoustic data were collected while the vessel ran at a nominal speed of 2.5 m s^{-1} over the summit and flanks along the 6-km-long transects that were oriented at 45° to one another (hereafter called summit transects; Fig. 1). Summit transects began and ended about 2 km beyond the summit edge (transect end depths, ca. 700–1000 m). Two complete sets (four transects/set) were usually completed during a night allocated for summit–transect surveys. Acoustic data from summit transects were partitioned into eight contiguous data cells of about 750 m along track lines [i.e., elementary sampling distance unit (ESDU)], equal to a 5-min time interval. These cells were subdivided vertically into either five or seven depth strata of 50 m each between depths of 10 and 260 m over the summit or 10 and 360 m over the flanks. The top 10 m of data were not used because reflections from near-surface air bubbles and the

ship's hull can adversely affect these data (Nero and Magnuson, 1989). Thus, each summit transect included 48 data bins except when extended to include SSL “plumes”.

To describe changes in the small-scale horizontal distributional patterns of the seamount-associated SSL over short time periods, contour plots of acoustic abundance were constructed for both the first and last half of each summit–transect survey night. Contours were based on estimates of depth-summed acoustic abundance that were determined over each ESDU between 10 and 260 or 260 and 360 m depths. Thus, for each night, four contour plots were generated to describe the SSL distributional pattern during the first and last half of the night, and above and below the summit depth. Reciprocal transects were conducted during a few nights, and mean values from these transects were then used with data from the remaining transects to generate the SSL contour plots. On two nights (9 August 1987 and 28 January 1988), only three in the set of four summit transects were completed.

To examine the association between the direction of the current and the direction in horizontal movement of the seamount-associated SSL on summit transect nights, the direction of net displacement of the contoured SSL from the first to the second part of a night was determined visually. The mean current direction was also determined on the same night from net displacements over the four deepest ADCP strata (114–210 m). Angular distance, which is the shortest distance between two points on a circle, was then determined for each pair of SSL and current angles. The Rayleigh test was performed on the angular distances to determine whether these were distributed randomly (Zar, 1984). In addition, differences between paired displacement angles of the SSL and current were examined with the Moore test for paired data on a circular scale (Zar, 1984). Comparisons between displacement angles of the SSL and currents were made with the SSL from above (10–260 m) and below (260–360 m) the summit.

Estimates of mean RAD for the seamount-associated SSL over the summit were compared with estimates at off-summit stations. Summit estimates were derived from the sets of four summit transects during the two nights allocated for acoustic surveys ($n = 2$ sets/night); no acoustic data from summit–flank

IKMT tows were used. Off-summit estimates were determined from the 5 and 10 km off-summit IKMT stations. The off-summit estimates combined the 5 and 10 km stations because no differences were observed during examinations among the 5 and 10 km station data within a cruise.

Nighttime vertical distributional patterns of the seamount-associated SSL were described from acoustic data taken during summit–transect surveys during each cruise. Only data collected between about 1.5 h after sunset and 2 h before sunrise were used.

The RAD estimates of the SSL were made during summit–flank IKMT tows to determine the relationship between density of acoustic scattering and net catches of *G. longispina* and *M. muelleri*. Estimates from either data set were for depths of about 10–260 m. The average ship speed during IKMT tows was about 1.5 m s^{-1} . RAD estimates were made over about 24 min after the net reached the maximum depth. In this manner, the RAD estimates roughly coincided with the times that the net was deeper than about 150 m (i.e., 160–260 m), which is the shallowest depth that relatively high numbers of seamount-associated micronekton were detected with acoustics and nets. For all statistical tests in this study, differences were considered significant at $p < 0.05$.

3. Results

3.1. Physical

Vertical temperature profiles of the surface waters around SE Hancock Seamount displayed characteristic seasonal differences. A strong vertical gradient in the seasonal thermocline was present during the summer, became reduced in the fall, and was less evident in the winter (Fig. 2). Surface water temperatures during the winter were about 19°C and the mixed layer extended to about 100 m deep. Surface temperatures during the summers increased to around 27°C and the depth of the mixed layer decreased to about 30 m. Water temperatures at the depth of the summit, however, only varied from about 13 to 15°C among the seasons.

Detailed results of current patterns are presented in Wilson (1992) but will be summarized here. During summer 1987 and winter 1988, the currents were generally unidirectional to the east and south, respectively, with mean current speeds of about 20 cm s^{-1} between depths of 40 and 210 m. During summer 1988 and fall 1988, mean speeds were less than 5 cm s^{-1} and much of the current field could be described as tidal rotary motions. Progressive vector plots con-

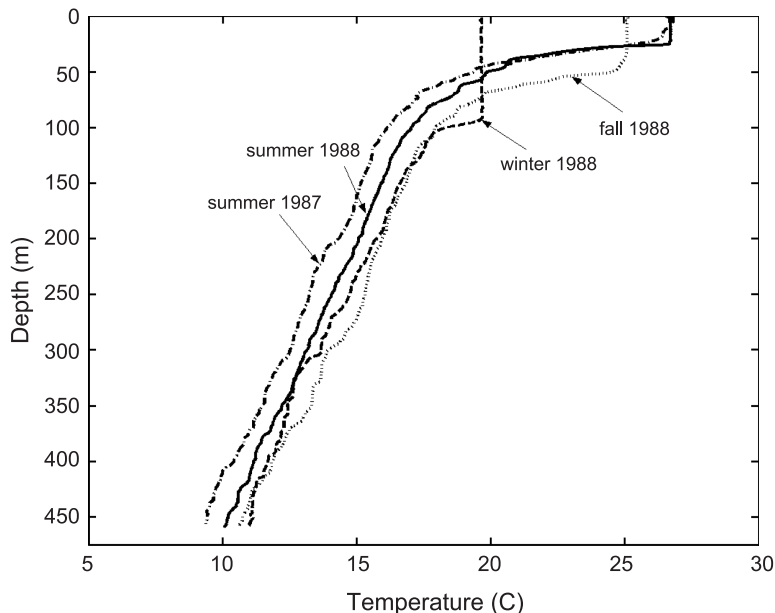


Fig. 2. Representative vertical temperature profiles at Southeast Hancock Seamount for the four cruises in 1987 and 1988.

structed for the nighttime period (1 h after sunset until 1 h before sunrise), when seamount-associated micro-nekton were often well above the summit, depicted the general trends in currents which were typical for each cruise (Fig. 3). During the last two cruises, net displacements were more broadly distributed around the summit than those from the first two cruises. The estimate of mean nighttime net displacement for summer 1987 was 6.1 km and for winter 1988 was 6.7 km; during the last two cruises, net displacements averaged only about one third those of the first two cruises (Table 1). On 1 of 10 nights in summer 1988 and four of nine nights in fall 1988, a significant vertical gradient in the horizontal velocity (i.e., verti-

Table 1

Estimates of nighttime mean current speed and net displacement over four depth strata (114–210 m) for each cruise

Cruise	Night period (h)	Net displacement (km)	Speed (cm/s)
Summer 1987, $n=36$	8.8	6.1 (1.8)	20 (5.6)
Winter 1988, $n=40$	11.5	6.7 (1.3)	16 (3.1)
Summer 1988, $n=44$	8.2	2.1 (0.8)	8 (2.2)
Fall 1988, $n=40$	11.1	2.4 (1.7)	9 (3.6)

Standard deviation listed in parentheses. Number of observations (n) is product between number of nights and the four depth strata.

cal shear) was present; on these nights, net displacement direction differences between two of the four depth strata could exceed 90° . More details on current

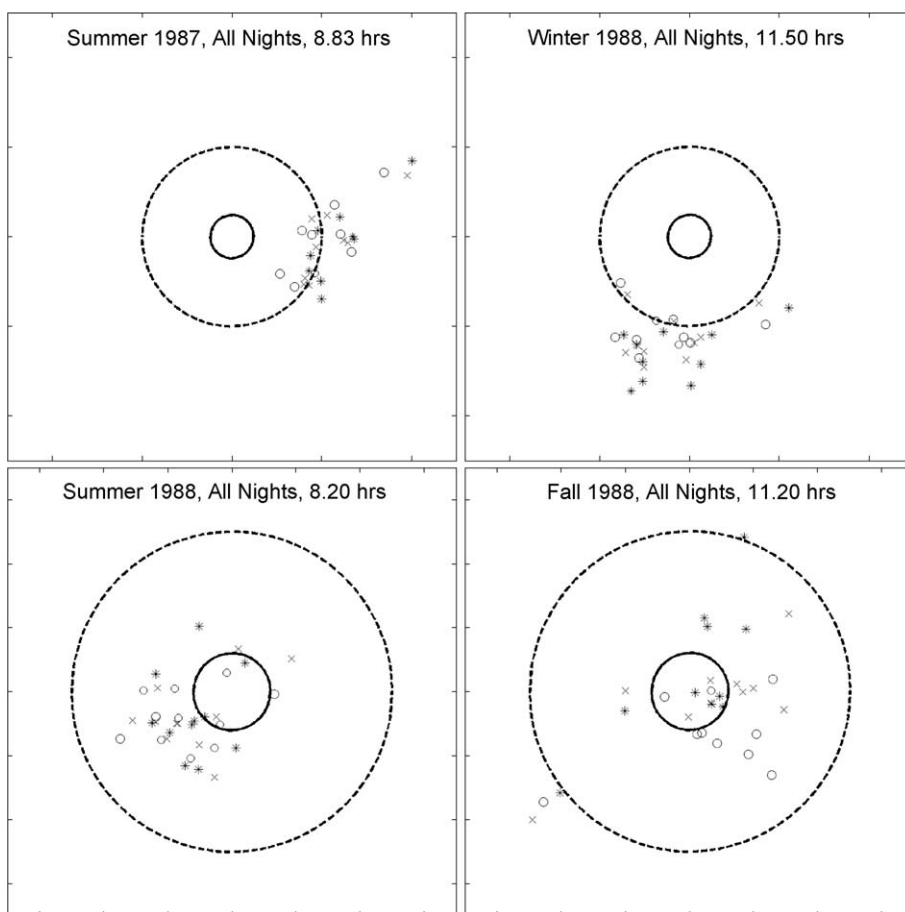


Fig. 3. Progressive current vector plots from the three deepest depth strata (*: 138–162 m; x: 162–186 m; O: 186–210 m) over Southeast Hancock Seamount summit for the nights during the four cruises in 1987 and 1988. Only the final positions are shown for clarity. The diameter of the smaller circle representing the summit is 2.4 km, and the larger circle is 10 km. Velocities are integrated over the entire night period with starting positions at the summit center.

patterns for particular nights are reported with the biological results.

Current meter data from an earlier study (Raugust et al., 1988) suggested that the deeper ADCP current estimates over the summit reflected closely the currents between 210 m and the summit (260 m). For example, comparison of current velocities from the summit current meter at 215 m with another at 255 m resulted in root mean square differences between eastward velocities (u) of 6 cm s^{-1} and northward velocities (v) of 7 cm s^{-1} . The plotted data indicated that at both depths, current directions were mostly within a single quadrant (Wilson, 1992). In general, this assumption allowed conclusions to be made when distributions of *M. muelleri* and *G. longispina* were centered deeper than the ADCP estimates, except under conditions of significant vertical shear on two nights in fall 1988 (discussed later).

3.2. Biological

Both *G. longispina* and *M. muelleri* were caught in IKMT tows during every cruise to SE Hancock Seamount. Net avoidance was not considered a problem because the length frequencies of *M. muelleri* taken in this study (Wilson, 1992) were similar to those noted in Boehlert et al. (1994), which included data from much larger nets. Abundances over the summit were greater than from the 5 and 10 km off-summit IKMT stations (Table 2). Neither

species was taken at off-summit stations during the first two cruises, and no *G. longispina* were ever taken at the 10 km off-summit stations. Acoustic data were collected from a total of 84 summit transects at night.

M. muelleri accounted for much of the acoustic signal of the seamount-associated SSL. Previous work at the seamount suggested that *M. muelleri* and *G. longispina* were the dominant micronekton species in the seamount-associated SSL (Boehlert, 1988a; Wilson, 1992). Net catches of *M. muelleri* from 27 IKMT tows over summit–flank zones were positively correlated with RAD estimates (Spearman $r=0.65$, $p<0.05$). *G. longispina* also exhibited a positive, although nonsignificant, association with RAD estimates (Spearman $r=0.20$, $p>0.05$). Other fishes, which could be considered relatively strong scatterers, were not significantly correlated with RAD estimates (Spearman $r=-0.31$, $p>0.05$; Wilson, 1992). Thus, RAD estimates were assumed an appropriate proxy for both *M. muelleri* and *G. longispina* despite the weak correlation with the latter species.

The abundance of the SSL over the summit based on acoustics showed trends that were similar to the net catch data. Among cruises, estimates of RAD at the summit were greatest in summer, declined in the fall, and further declined in winter. They always exceeded estimates made 5–10 km away from the summit (Table 2). The RAD estimates from the off-summit stations were only about 10–20% of the summit values during the summers and fall. During the winter, the proportion increased to 40% because of the decreased scattering at the summit and the increased scattering away from the summit.

Vertical distributional patterns of *M. muelleri* and *G. longispina* from IKMT catches were generally similar and indicated greatest abundance of both species within 100 m of the summit (Fig. 4). The median number per tow in the two shallow strata, over all cruises, was significantly different from that in the deeper strata for *G. longispina* (Mann–Whitney U -test, $p=0.002$) and *M. muelleri* (Mann–Whitney U -test, $p=0.006$).

Vertical distribution patterns of the seamount-associated SSL based on acoustic estimates were generally consistent with net catches and complemented net

Table 2
Estimates of density (per 10^4 m^3) for *M. muelleri* and *G. longispina* from net catches and of relative acoustic density (RAD) for the sound scattering layer over the summit and 5–10 km away from the summit

Survey	Summit			Off-Summit		
	<i>M. muelleri</i>	<i>G. longispina</i>	RAD	<i>M. muelleri</i>	<i>G. longispina</i>	RAD
Summer 1987	2.68	26.43	43.0	0	0	7.0
Winter 1988	1.65	10.90	29.0	0	0	12.0
Summer 1988	5.28	72.63	44.0	0.12	0.07	4.0
Fall 1988	1.38	41.53	34.0	0	0.37	3.0

Catch estimates over the summit are the averages of estimates from horizontal tows, while those at 5–10 km away are oblique hauls.

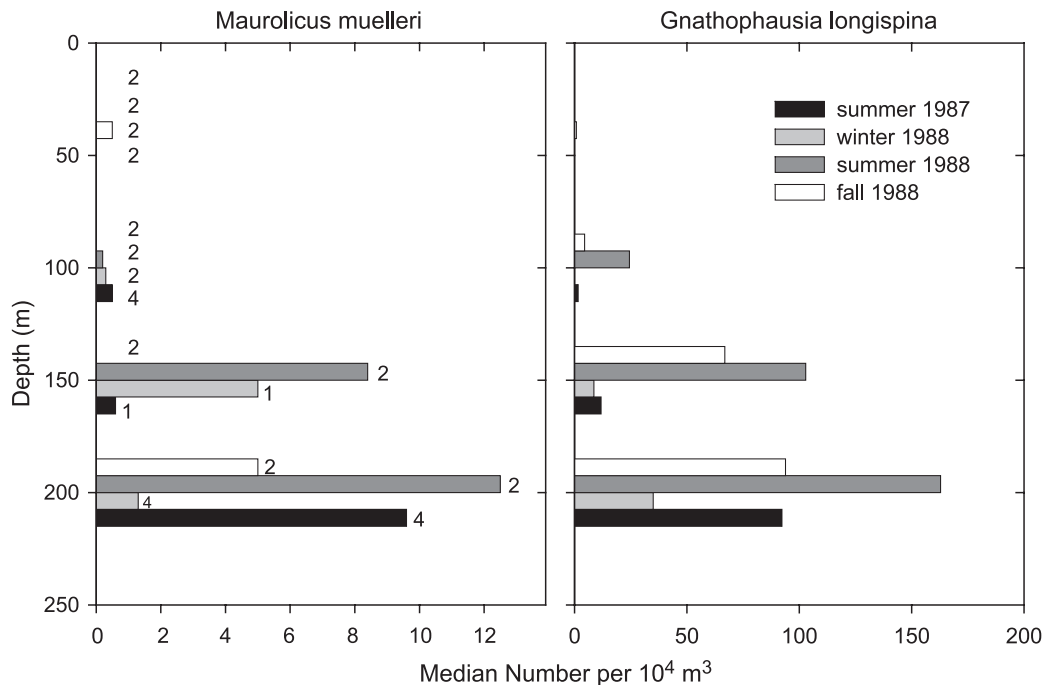


Fig. 4. Vertical distribution of *M. muelleri* and *G. longispina* over Southeast Hancock Seamount summit based on trawl data for the four cruises in 1987 and 1988. Numbers of hauls are listed at bar head.

data by providing more spatial resolution, greater coverage per unit time, and data to greater depths (Fig. 5). On all cruises, relatively little scattering occurred above 150 m depth. Similar to the IKMT results, the RAD increased with depth approaching the summit. Only in summer 1987, however, did values continue to increase with depth below the summit. The fraction of the total acoustic scattering between 10 and 360 m depth that occurred above the summit varied among cruises; thus, the proportion of total scattering between the summit and the ocean surface was 33% for the summer 1987, 54% for the winter 1988, 48% for the summer 1988, and 64% for the fall 1988 (Fig. 5). The slightly greater values in fall and winter may be related to variations in the distribution and abundance of *M. muelleri* (see Discussion). The scattering below the summit was not necessarily confined close to the seamount flanks but sometimes extended laterally from the seamount to distances of 1 km or more. It is noteworthy that around sunset, the seamount-associated SSL has often been detected rising from seamount flank regions in the depth range where much of the SSL below the

summit is found later during the night (Boehlert, 1988b).

The vertical distributional patterns based on either net catches or acoustics did not provide evidence that *M. muelleri* or *G. longispina* reduced their movements above the summit in response to increased current speeds. The seamount-associated RAD above the summit (10–260 m) was expressed as a proportion of the total scattering (10–360 m) for each night of summit–transect surveys (two per cruise). When these proportions were plotted as a function of current speed across all cruises, no significant association was detected (Spearman $r = -0.310$, $p > 0.05$). Although the proportion of scattering from above the summit decreased with increasing current speeds for the summer data (range, 7–22 cm s^{-1}), this was not the case in winter 1988 when a relatively large proportion of scatterers were above the summit on a night with strong currents (18 cm s^{-1}).

Results from the net data demonstrated that horizontal small-scale distributional patterns of *M. muelleri* and *G. longispina* over the summit were influenced by currents. A total of 30 IKMT tows were conducted over

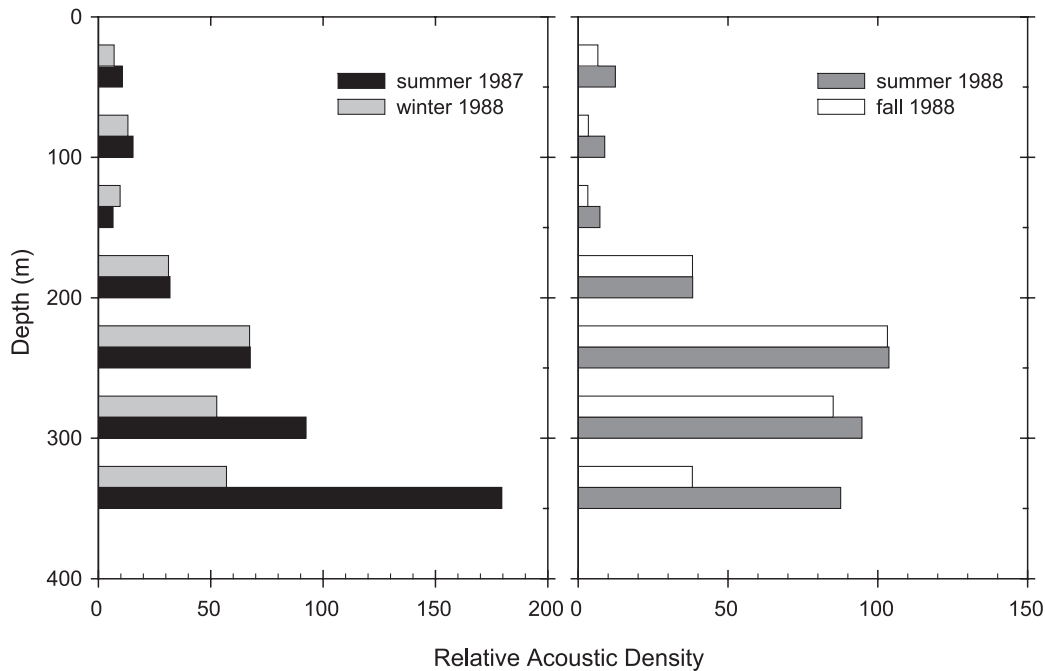


Fig. 5. Vertical distribution of relative acoustic density estimates of the sound scattering layer over Southeast Hancock Seamount summit and flanks for the four cruises in 1987 and 1988. See text for acoustic density estimation procedure.

downstream (14 tows) versus other summit–flank regions (16 tows) for all cruises. In this discussion, we exclude from consideration those surveys and samples where significant current shear or rotary currents prevented a clear definition of upstream and downstream. During the first two cruises, mean current speeds on nights of summit–flank tows ranged from 15 to 30 cm s^{-1} . These currents produced nighttime net displacements that could potentially move animals at least 5 km downstream during the night. On nights when tows were made during the third cruise, mean current speeds were less, 8–10 cm s^{-1} , although mean net displacements still exceeded 1.5 km. On these cruises, catches of *M. muelleri* and the SSL acoustic densities were significantly greater over the downstream summit–flanks (Table 3). Catches of *G. longispina* also exhibited a strong trend of greater numbers downstream; catches downstream exceeded those over other summit–flanks, except for one set of paired tows on 23 July 1988 (101.5 vs. 295.0, Table 3).

The small-scale horizontal distribution of the seamount-associated SSL generally appeared fairly well contained over the summit and summit–flank zones

during most nights of summit–transect acoustic surveys. On many transects, acoustic backscatter from seamount-associated SSL diminished to levels similar to those away from the summit near the end of the 6 km transect (about 3 km from the summit center). Furthermore, the decrease in the seamount-associated SSL intensity often occurred fairly quickly.

The seamount-associated SSL was often displaced to the downstream side of the summit by the end of the night. These results were consistent among cruises and corroborated results from summit–flank IKMT tows. The night of 28 October 1988 was exceptional in that a strong vertical current shear was present. This night, discussed later, was treated separately from the other seven nights of summit–transect data because of the complicated current patterns. Representative results for other nights on each cruise are presented below. Most emphasis is placed on the distributional patterns of the SSL above the summit (10–260 m depth) rather than below the summit (260–360 m). Animals below the summit might be exposed to current patterns that are quite different from the estimates above the summit

Table 3

Densities (per 10^4 m^3) of *M. muelleri* and *G. longispina* from trawl hauls (0–260 m) and their relative acoustic density (see text) over downstream summit–flanks versus other summit–flanks

Density by summit–flank location							
Date	Mean current direction	<i>M. muelleri</i>		<i>G. longispina</i>		Relative density (acoustic)	
		Downstream	Other	Downstream	Other	Downstream	Other
<i>Summer 1987</i>							
08 Aug.	SE	1.9, 0.0	0.0	31.1, 0.9	0.0	high ^a , med ^a	low ^a
21 Aug.	E	3.5, 8.1	0.9, 0.0, 0.7	179.5, 16.2	12.6, 3.1, 0.0	50, 72	17,16,17
25 Aug.	ENE	0.0	0.0, 0.0	40.9	16.1, 6.3	15	6, 19
<i>Winter 1988</i>							
28 Jan.	SE	1.7, 0.4	1.3, 0.0	111.4, 110.8	0.0, 0.0	18, 17	8, 7
<i>Summer 1988</i>							
15 Jul.	SW ^b	3.3	0.0	316.0	44.7	15	4
23 Jul.	N ^b	0.5, 19.2	0.0, 1.6	128.0, 101.5	100.0, 295.0	8, 41	5, 5
21 Aug.	N	0.4	0.0	109.5	39.6	29	3
		<i>p</i> = 0.012		<i>p</i> = 0.086		<i>p</i> = 0.012	
<i>Fall 1988</i> ^c							
29 Oct.	V ^{b,d}	0.5, 28.5	0.5, 4.8	152.1, 128.4	105.8, 96.9	4, 43	39, 26
07 Nov.	SE	31.6 ^e	0.0 ^f , 0.4 ^f	94.8 ^e	6.7 ^f , 3.7 ^f	42 ^e	5 ^f , 3 ^f

Each number represents one tow.

^a Visual estimate from the echo–sounder paper trace.

^b Represents current estimate from fitted tidal model.

^c Data excluded from statistical tests.

^d Currents with strong vertical shear; direction variable, e.g., Fig. 9a; number pairs in left or right column from SW or NE summit–flank, respectively; 2nd value of each pair from horizontal tow.

^e Conducted over SW summit–flank.

^f Conducted over NE summit–flank.

because of increased current–topography interactions near the summit (Roden, 1987). Nonetheless, distributional shifts in the SSL from 260 to 360 m were often similar to those above the summit.

Results from a night in summer 1987 (19 August) and another in winter 1988 (15 January) displayed the characteristic shifts in the SSL to downstream summit–flank regions (Fig. 6). On these nights, ocean current speeds were reasonably strong and averaged 22 cm s^{-1} to the east for the summer 1987 and 14 cm s^{-1} to the south for the winter. During the first half of both nights, the SSL above the summit was distributed over the entire summit (Fig. 6a,c). By the latter half of the night, however, most scattering had been displaced downstream of the summit (Fig. 6b,d).

Currents were slower during the summer 1988 cruise, but the SSL still moved to the downstream summit–flank regions over the course of a night. On the night of 13 July 1988, for example, current speeds

were 10 cm s^{-1} to the southwest. During the first part of the night, the SSL distribution was centered over the summit, but by the second half of the night, the scatterers had expanded downstream to the southwest (Fig. 7a,b).

Although rotary currents complicated the interpretation of the SSL distribution for one night of summit–transect surveys in fall 1988 (see below), the other night (4 November) was consistent with patterns seen on previous cruises. On this latter night, current speed was 8 cm s^{-1} as determined from trajectory lengths (1 cm s^{-1} based on net displacement), although net displacements were small and to the east. Nonetheless, the SSL was broadly distributed over the west–southwest side of the summit and flanks during the first part of the night, and by the second part of the night, animals had moved slightly to the east and were more uniformly distributed over the entire summit (Fig. 7c,d).

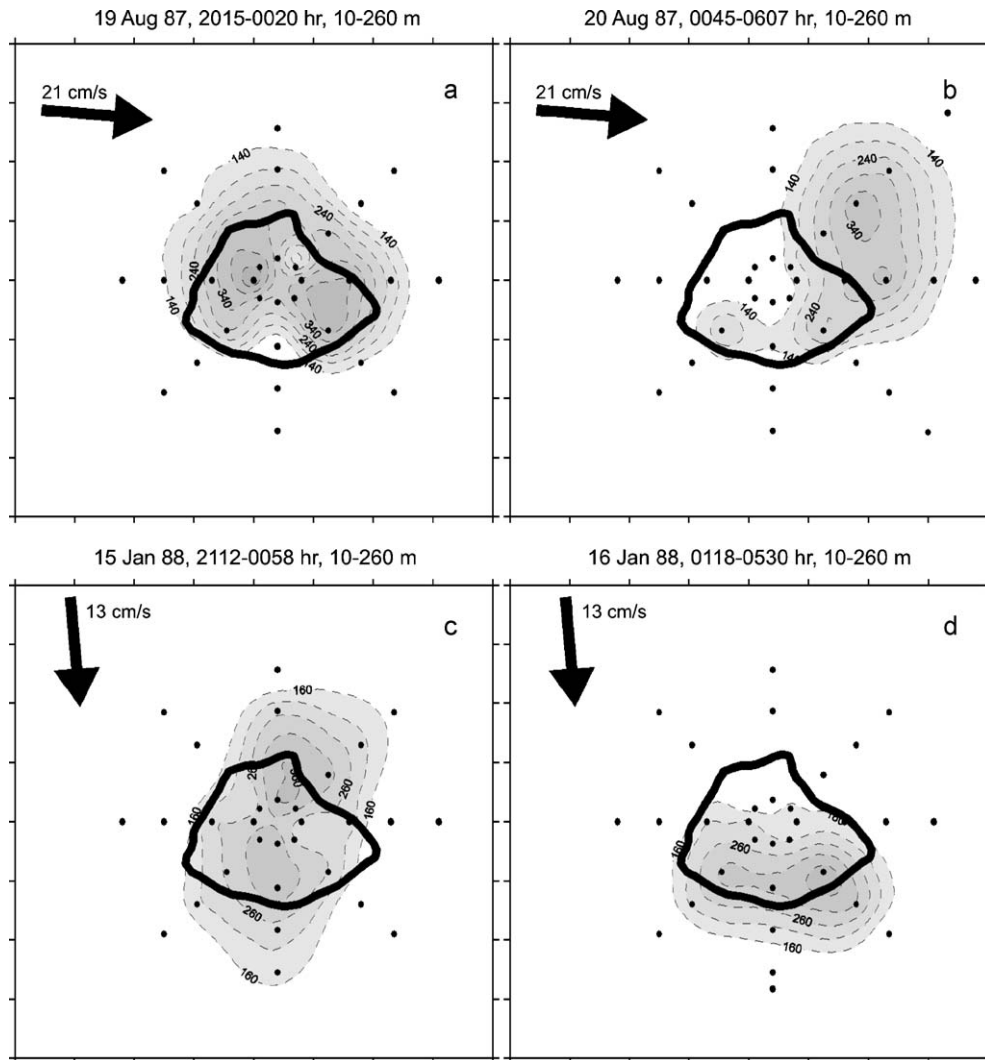


Fig. 6. Contoured relative acoustic abundance estimates of the sound scattering layer above Southeast Hancock Seamount summit from the first (a, c) and last (b, d) part of a representative night for the summer 1987 (a, b) and winter 1988 (c, d) cruises. Mean estimate of ocean current direction (arrow) and speed, based on net displacement, for the 114–210 m depth range is shown for the same night. The solid line is the 300 m bottom contour. Axes tick mark spacing is 0.01 latitude or longitude (about 1 km).

The seamount-associated SSL below the summit was often displaced in the direction that was consistent with the current direction above the summit. For the winter 1988 example above (Fig. 6c,d), the deeper SSL was also most abundant over the upstream and downstream flanks during the first part of the night and, by the latter part of the night, had been displaced downstream toward the south (Fig. 8). On a few other nights, interpretation of the shift

in the SSL distribution was not as obvious. For the fall 1988 example presented earlier, currents were slower, and the deeper SSL was not displaced to the east side of the summit during the last part of the night (not shown). Whether this was due to the blocking effect of the summit, slow currents, or other factors is unknown.

Generally, the same pattern in downstream displacement of the seamount-associated SSL was

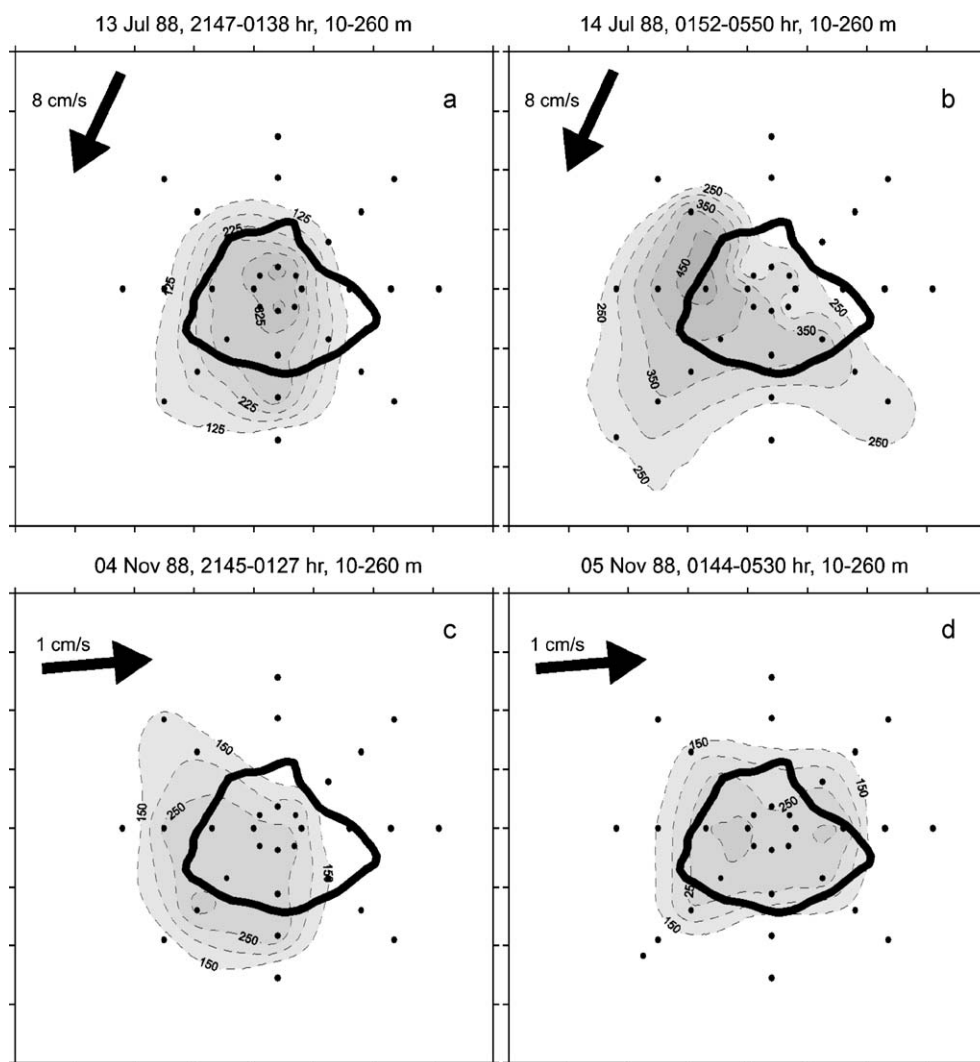


Fig. 7. Contoured relative acoustic abundance estimates of the sound scattering layer above Southeast Hancock Seamount summit from the first (a, c) and last (b, d) part of a representative night for the summer 1988 (a, b) and fall 1988 (c, d) cruises. Figure details as in Fig. 6.

observed on other summit–transect nights on all cruises. To more quantitatively assess this relationship, the data were subjected to two statistical tests. Angular distances between direction of net displacement for currents and those of the SSL above and below the summit depth were determined (Table 4). The angular distances based on the SSL above the summit were not randomly distributed (Rayleigh, $p < 0.001$) and, in fact, rarely exceeded about 30° . This was regardless of whether currents were to the east or south (Table 4). When data for the SSL

above the summit were then subjected to the Moore test for paired observations on a circular scale, there was insufficient evidence to suggest that paired displacement angles of the current and SSL were drawn from different populations ($p \gg 0.2$, Table 4). This provided further support that the water and the SSL above the summit moved in similar directions.

Similar conclusions were reached with regard to the SSL below the summit. However, the mean angular distance was greater for the deeper SSL than

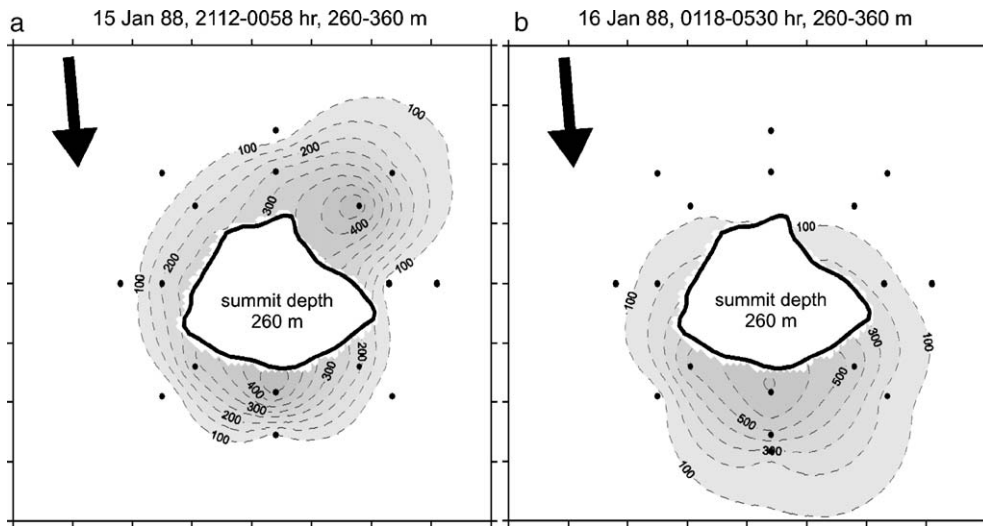


Fig. 8. Contoured relative acoustic abundance estimates of the sound scattering layer below Southeast Hancock Seamount summit from the first (a) and last (b) part of a representative night for the winter 1988 cruise. Figure details as in Fig. 6.

for the SSL above the summit, primarily because of the larger differences in displacement directions of the currents and the SSL during the last two cruises when the currents were generally weaker (Table 4). Nonetheless, angular distances were not randomly distributed, nor was there any evidence to conclude that paired displacement angles between the ocean cur-

rents and the deep SSL were significantly different (Table 4).

Some nights in summer 1988 and fall 1988 were characterized by strong vertical current shear that complicated interpretation of the data on animal distributions. For example, this was evident during net sampling over the summit–flank zones on 29 October 1988. On this night, ocean current net displacements were of similar magnitude but were in dramatically different directions (Fig. 9a). At 114–138 m depth, net flow was to the north, whereas at 186–210 m, the direction was reversed. Given the strong vertical shear to the 210 m depth and anticyclonic rotation of the current, it appears that deeper currents would have a strong southward component. The SSL changed from early to late sampling periods, with a southward drift and clockwise rotation (Fig. 9b,c).

Table 4

Displacement angles for currents (WA) and the seamount-associated sound scattering layer (SSL) from 10–260 m (SSL₂₆₀) and 260–360 m depth (SSL₃₆₀) for nights of summit–transect surveys on four cruises at Southeast Hancock Seamount

Night	WA	AD ₂₆₀	SSL ₂₆₀	AD ₃₆₀	SSL ₃₆₀
09 Aug 1987	121	5	116	42	163
19 Aug 1987	92	28	64	14	106
15 Jan 1988	170	9	161	33	203
27 Jan 1988	205	31	174	3	202
13 Jul 1988	203	31	234	21	182
21 Jul 1988	217	65	152	94	123
04 Nov 1988	71	20	51	127	304
Mean AD	27			44	
Rayleigh test		$z = 6.32$		$z = 3.99$	
		$p < 0.001$		$p < 0.02$	
Moore test		$R' = 0.710$		$R' = 0.354$	
		$p \gg 0.2$		$p \gg 0.2$	

Also given are angular distances (AD) between current and SSL angles, and results of statistical tests. The Rayleigh test was performed on ADs, and the Moore test was performed on displacement angle pairs.

4. Discussion

Physical processes, especially currents, play a major role in determining the abundance and distributional patterns of marine organisms that are variously associated with banks and seamounts (Boehlert and Genin, 1987; Loder et al., 1988). Although some seamount studies have integrated information on cur-

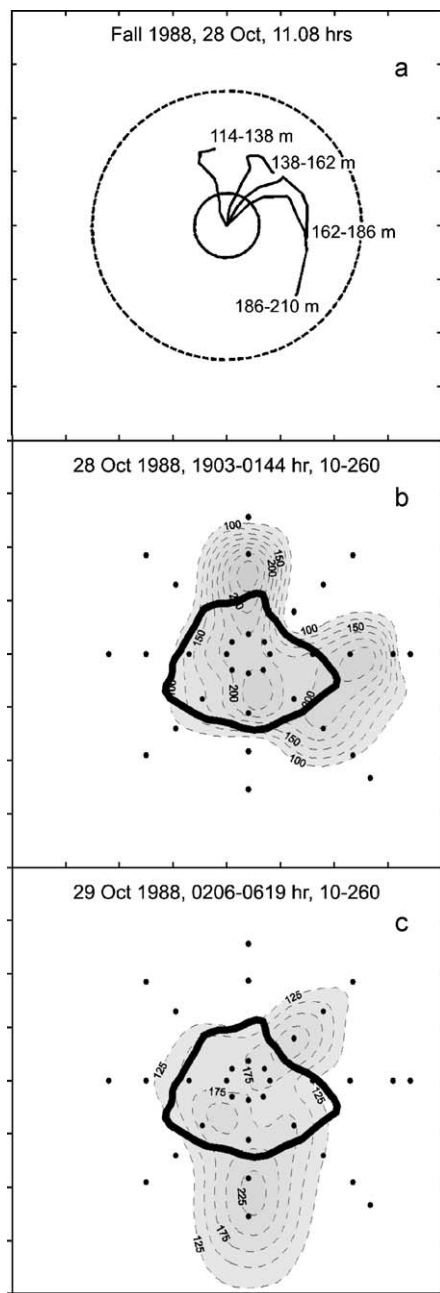


Fig. 9. Progressive current vectors for the four deepest depth strata (a) and contoured relative acoustic abundance estimates of the sound scattering layer, over Southeast Hancock Seamount summit for the first (b) and last (c) part of the night of 28 October 1988. Net displacements over the entire night period for the depth strata ranged between 2.6 and 3.7 km. Figure details as in Figs. 3 and 6.

rents with biological findings, these studies have primarily focused on benthic (Genin et al., 1986) or planktonic organisms (Genin and Boehlert, 1985; Dower and Perry, 2001) with relatively little effort directed at the mesopelagic micronektonic species (Boehlert, 1988a). Because micronekton may move into waters above the seamount on a diel basis, physical processes might have significant effects on their distribution with processes that may differ from those on continental shelves (Pereyra et al., 1969) or islands (Benoit-Bird et al., 2001). The present study demonstrates how currents affect the small-scale micronekton distributions, in this case, *M. muelleri* and *G. longispina*, over the SE Hancock Seamount summit. Both species were able to maintain local populations at the summit throughout the year. *M. muelleri* and *G. longispina* form part of a community of “mesopelagic-boundary” micronektonic animals that inhabit a narrow zone between the oceanic mesopelagic, and continental, island, or seamount slopes (Reid et al., 1991). Insight into the processes involved in the maintenance of such seamount-associated populations may provide increased understanding of the processes important in the formation and maintenance of boundary communities in other geographical areas (Parin, 1986; Reid et al., 1991; Benoit-Bird et al., 2001).

4.1. Population maintenance

Various studies have identified micronektonic taxa associated with continental or island slope habitats (reviewed in Gjosaeter and Kawaguchi, 1980; Reid et al., 1991). The present study identified *M. muelleri* and *G. longispina* as the dominant, recurrent members of the micronektonic community over the small summit at SE Hancock Seamount regardless of the year, season, or hydrographic regime. Both species were largely absent from the surrounding oceanic waters 5–10 km from the summit. The absence of these species in the subtropical central North Pacific well away from the Northern Hawaiian–Southern Emperor Ridge (Barnett, 1975; Loeb, 1979) suggests that these species form a permanent part of the micronektonic seamount community at SE Hancock Seamount.

Over short time and small-space scales, however, the distributions of *G. longispina* and *M. muelleri* at

the summit were affected by currents. As is characteristic of this region of the Pacific (Roden, 1987; Roden et al., 1982), currents were quite variable among cruises and ranged from relatively strong nearly unidirectional currents to weaker, mostly rotary motions (Wilson, 1992). The differences in currents are evident in progressive vector diagrams; nighttime net displacements averaged 6–7 km per night during the first two cruises and only about 2 km per night for the last two cruises (Table 1, Fig. 3). Regardless of differences in nighttime currents, however, animals were usually displaced to the downstream side of the summit by the end of the night (Figs. 6–8). In spite of these nightly displacements, the population occurred above the summit on subsequent nights. Furthermore, on most nights during the first two cruises, the SSL displacement downstream was markedly less than that predicted from the currents, suggesting directed swimming similar to that seen in other studies (Benoit-Bird et al., 2001). On the last cruise, vertical shear in horizontal velocities was so strong on some nights that it complicated the interpretation of the species' distributional patterns. On these nights, currents at different depths were similar in speed but very different in direction (e.g., Fig. 9). As discussed later, this shear might actually contribute to the population maintenance of *G. longispina* and *M. muelleri*.

Population maintenance of *G. longispina* and *M. muelleri* at SE Hancock Seamount is based upon a combination of physical and behavioral mechanisms. Although *M. muelleri* and *G. longispina* are taxonomically and morphologically dissimilar, the differences in nighttime distribution patterns of these two species were relatively slight and suggest similarities in behaviors involved in population maintenance on short time scales. Close associations and similar behaviors are known to exist between fish and mysids, particularly when they are of similar size (McFarland and Kotchian, 1982). In our study, *M. muelleri* and *G. longispina* generally moved similar distances above the summit at night, although in winter, catches of *M. muelleri* extended to the ocean surface (Wilson, 1992). Both species were rarely found far from the summit: *G. longispina* was never caught 10 km from the summit, and at the 5 km station, it was caught in numbers similar to *M. muelleri* although summit catch rates for *G. longispina* were an order of magnitude greater than *M. muelleri*.

Nighttime vertical distribution patterns of both *M. muelleri* and *G. longispina* indicated that most animals were found within 100 m of the summit. The seasonal thermocline did not appear important in defining the limits of their upward movements (Figs. 2, 4, 5). In other studies, thermal gradients have been important in defining the vertical distribution patterns of various species (for review, see Neilson and Perry, 1990). Barange et al. (1991), for example, observed different migration patterns relative to the thermocline in two species of euphausiids.

Neither *G. longispina* nor *M. muelleri* were observed to reduce their vertical movements above the summit with increased current speeds as a possible mechanism for population maintenance. Other workers have observed this type of response in fish (Hobson and Chess, 1976), mysids (Kaartvedt, 1989), euphausiids (Liljebladh and Thomasson, 2001), and zooplankton (Wooldridge and Erasmus, 1980). Whether stronger current speeds than observed in this study (i.e., maximum about 25 cm s^{-1} on nights of depth stratified sampling) would elicit a response from *G. longispina* or *M. muelleri* is unknown. Current speeds in the above cited studies, however, were generally quite strong, ranging from 38 to 80 cm s^{-1} (Wooldridge and Erasmus, 1980; Butman and Beardsley, 1987).

Numerous studies have considered vertical migration patterns as a means of population retention through exposure to differential current directions (Hardy, 1956; Peterson, 1998). The vertical gradient in horizontal velocity (i.e., vertical shear) may periodically offer a similar advantage to seamount micronekton. On several occasions, most notably during summer 1987, progressive vector plots documented a slight decrease in net displacement with depth over the four deepest strata, although displacement directions were still similar. During several nights in fall 1988, however, final positions from progressive vector plots differed by nearly 180° between some depth strata (e.g., Fig. 9). Neither acoustic nor net sampling tracks the movement of individuals within the SSL. Thus, *M. muelleri* and *G. longispina* may change depths throughout the night and experience differences in horizontal flow. Intraspecific diel vertical distribution patterns of fishes and crustaceans are often variable (Neilson and Perry, 1990). For example, some individuals may not migrate every night but

remain at their deeper daytime depths (Pearcy et al., 1977; Haury, 1988). Clarke (1982) suggested that this pattern may occur in *M. muelleri*. No studies have investigated the degree of vertical movement at night by mesopelagic fauna within their “shallower” nighttime depth range except for some preliminary work by Clarke (1973) who found no evidence that myctophids underwent a “midnight dispersal” in near surface Hawaiian waters, and Kaartvedt (1989) who reported that numbers of the mysid *Lophogaster typicus* moved among depths during the night. Although the vertical dimensions of the summit SSL remained fairly uniform during most nights, this does not necessarily imply that individuals are maintaining a particular depth (Pearre, 1979). Thus, the species’ complicated spatial distribution on some nights (e.g., Fig. 9) may have produced the variable net catch data (29 October, Table 3) as a result of strongly baroclinic currents interacting with the vertical nighttime movements of individuals of *M. muelleri* and *G. longispina*.

Another possible mechanism that may be important for *M. muelleri* and *G. longispina* to avoid advection from the summit may be by swimming upslope along the bottom during the day in a two-phase movement as suggested by Benoit-Bird et al. (2001). Animals advected off the summit could descend to bottom waters at the seamount flank. They could orient in an upflank direction and move summitward such that by nightfall, they would again be concentrated at preferred depths on the slope. Clarke (1982) reported that diel differences in the distribution of *M. muelleri* from the continental shelf off Australia were consistent with upward and inshore (thus, upslope) movements. Unfortunately, little is known regarding the daytime distribution patterns for either of these two species at SE Hancock Seamount.

The ADCP provided evidence to suggest that behavioral responses on the part of *M. muelleri* and *G. longispina* may be important in population retention. The dominant acoustic scatterers 50–100 m above SE Hancock Seamount summit (likely *M. muelleri*) exhibited coherent horizontal movements at sunrise, possibly to counteract advection from the summit (Wilson and Firing, 1992). These movements were identified during the last two cruises as large residual velocities that occurred at sunrise between the observed ADCP current estimates and those of a fitted tidal model. It might be that *M. muelleri* and possibly

G. longispina are able to orient and move in an upstream direction. In situ observations on other mysid species have included active swimming into currents to maintain position (Robertson et al., 1968). How this is accomplished 50 m or more above SE Hancock Seamount by either *M. muelleri* or *G. longispina* is unknown although mechanisms have been suggested (Wilson and Firing, 1992).

The continual presence of both *G. longispina* and *M. muelleri* at the seamount suggests that there are selective advantages conferred upon both species as seamount residents. One benefit may be increased feeding success, where currents transport oceanic prey species into or over the seamount (Isaacs and Schwartzlose, 1965). Information from other studies suggests that the feeding ecology of *G. longispina* and *M. muelleri* may explain their nighttime distributions above the summit despite the increased risk of advection away from the seamount. In many other areas, *M. muelleri* feeds primarily at night (Young and Blaber, 1986) or during crepuscular periods (Dalpadado and Gjosaeter, 1987b). At SE Hancock Seamount, *Pleuromamma* spp. are a major dietary item of *M. muelleri* (J. Hirota, unpublished data), and based upon work from other areas (Bennett and Hopkins, 1989), *Pleuromamma* spp. are most abundant at night over depths of less than 150–200 m. Thus, maximum densities of this prey species may be encountered by *M. muelleri* when nighttime excursions are made to these shallower depths above the summit. High growth rates at the seamount corroborate this hypothesis (Boehlert et al., 1994). Similar trends have been reported to explain the nighttime distribution patterns of oceanic crustaceans (Pearcy, 1970; Barange et al., 1991), which raises the possibility of an analogous scenario for *G. longispina*.

4.2. Population stability and life history contrasts

Short-term distributional patterns for *M. muelleri* and *G. longispina* at SE Hancock Seamount are generally very similar. Both species usually moved to similar nighttime depths above the summit (Fig. 4, but see below), both were often in greater abundance over the downstream summit–flank regions (Table 3), and both were rarely caught far from the summit. However, a few notable differences were observed in comparisons among seasons, particularly with the

winter results for *M. muelleri*. These differences likely reflect the differences in life history patterns of the two species.

M. muelleri is apparently an annual population at SE Hancock Seamount (Boehlert et al., 1994), in contrast to populations in other geographical areas where *M. muelleri* might live up to 4 years of age (Gjosaeter, 1981). The population size composition of *M. muelleri* over all seasons at the seamount suggests that the smallest fish are present in the spring have reached their largest sizes by winter but are absent by the following spring. Advective losses from the seamount probably combine with losses from predation to explain the apparent winter loss of *M. muelleri* from the seamount. The fish were generally higher in the water column during the winter than in other seasons, increasing the risk to predation from epipelagic predators and advective losses from the seamount. This is supported by the observation that *M. muelleri* were taken at the ocean surface only during the winter (Wilson, 1992). Similarly, the fraction of acoustic scattering above the summit (10–260 m), as a proportion of the total scattering (10–360 m) was greatest in the fall and winter rather than summer. It is noteworthy that the shallowest *M. muelleri* specimens from the summit were large; the median length of *M. muelleri* from neustonic catches (median = 44 mm SL, mean = 44, S.D. = 1.9, $n = 44$) was significantly different (Mann–Whitney U -test, $p = 0.05$) than that from horizontal IKMT tows at least 150 m deep (median = 42 mm SL, mean = 43, S.D. = 2.4, $n = 30$). Boehlert et al. (1994) observed larger *M. muelleri* up to 40 km from the seamount in August, and suggested that the annual population of *M. muelleri* at SE Hancock Seamount is apparently dependent on recruitment of young from other areas such as the large seamounts in the Southern Emperor range.

G. longispina is probably a more ‘long-term’ resident at the seamount than *M. muelleri* and consequently loses fewer individuals from the summit during winter or other times. Larvae of *G. longispina* are brooded in a maternal marsupial pouch and are later released as young that superficially resemble small adults. This reproductive mode is considered to promote retention, which is consistent with benthic species on many seamounts (Parker and Tunncliffe, 1994). Evidence suggests that all instar stages are present at the SE Hancock Seamount (Wilson and

Boehlert, 1993), whereas for *M. muelleri*, the smaller postmetamorphic sizes are rare. *G. longispina* lives for at least 2 years at the seamount and is probably dependent on local recruitment for its persistence (Wilson and Boehlert, 1993). Thus, a mode in the population size composition that represents the largest size class for *G. longispina* is well represented over all seasons although addition of individuals to this size class through growth is restricted to the summer months (Wilson and Boehlert, 1993).

Other data provide further evidence that *G. longispina* may be a longer-term seamount resident than *M. muelleri*. Unlike *M. muelleri*, numbers of *G. longispina* from depth stratified tows always decreased with distance above the summit (Fig. 4), and no specimens were ever taken in neuston tows. As mentioned earlier, greater numbers of *G. longispina* than *M. muelleri* were taken over the summit, although numbers of both species from off-summit stations were about equal. Furthermore, no *G. longispina* were taken at distances as far from the summit as *M. muelleri*. No other large populations of *G. longispina* have been found near Hancock Seamount, which also suggests that local recruitment maintains this mysid population (Wilson and Boehlert, 1993).

Complex flow-topography interactions at seamounts, such as trapped eddies or Taylor Columns, have been considered as possible retention mechanisms that enable large populations of organisms to exist over seamounts (Shomura and Barkley, 1980; Boehlert and Genin, 1987; Dower and Perry, 2001). It is doubtful that these hydrographic features are directly responsible for retaining micronektonic animals, such as *G. longispina* or *M. muelleri*, at the seamount (although enhancement of lower trophic levels might be indirectly beneficial). Observations of Taylor Columns or flows reminiscent of these features have generally been on spatial scales larger than the scale of the population of either of these species at the summit (Brainard, 1986; Wilson, 1992). It is more likely that the continued nightly presence of both species above the relatively restricted summit area in the presence of currents suggests that directed swimming behaviors, combined with small-scale hydrographic features, such as reduced flow in the lee of the seamount, are of greater importance than Taylor Columns in maintaining these two populations.

Acknowledgements

This research was conducted while the authors were at the NMFS Honolulu Laboratory and the support from NOAA for this study is gratefully acknowledged. The research formed part of the PhD dissertation for C.D. Wilson. We thank the officers and crew of the NOAA vessel *Townsend Cromwell* for their support during the cruises to Hancock Seamount and to many of the scientific staff of the Honolulu Laboratory Seamount Research Program, including M.P. Seki and R.L. Humphreys.

References

- Armstrong, M.J., Prosch, R.M., 1991. Abundance and distribution of the mesopelagic fish *Maurolicus muelleri* in the southern Benguela system. *S. Afr. J. Mar. Sci.* 10, 13–28.
- Backus, R.H., Craddock, J.E., Haedrich, R.L., Shores, D.L., Teal, J.M., Wing, A.S., Mead, G.W., Clarke, W.D., 1968. *Ceratoscopelus maderensis*: peculiar sound-scattering layer identified with this myctophid fish. *Science* 160, 991–993.
- Bakun, A., 1988. Local retention of planktonic early life stages in tropical demersal reef bank systems: the role of vertically-structured hydrodynamic processes. IOC/FAO Workshop on Recruitment in Tropical Coastal Demersal Communities, Ciudad del Carmen, Campeche, Mexico. April, 1986. IOC Workshop Report, vol. 44, pp. 15–32. Supplement.
- Barange, M.G., Gibbons, M.J., Carola, M., 1991. Diet and feeding of *Euphausia hanseni* and *Nematoscelis megalops* (Euphausiacea) in the northern Benguela current: ecological significance of vertical space partitioning. *Mar. Ecol., Prog. Ser.* 73, 173–181.
- Barnett, M.A., 1975. Studies on the patterns of distribution of mesopelagic fish faunal assemblages in the central Pacific and their temporal persistence in the gyres. PhD dissertation, Univ. Calif., San Diego.
- Bennett, J.L., Hopkins, T.L., 1989. Aspects of the ecology of the calanoid copepod genus *Pleuromamma* in the eastern Gulf of Mexico. *Contrib. Mar. Sci.* 31, 119–136.
- Benoit-Bird, K.J., Au, W.W.L., 2001. Target strength measurements of Hawaiian mesopelagic boundary community animals. *J. Acoust. Soc. Am.* 110, 812–819.
- Benoit-Bird, K.J., Au, W.W.L., Brainard, R.E., Lammers, M.O., 2001. Diel horizontal migration of the Hawaiian mesopelagic boundary community observed acoustically. *Mar. Ecol., Prog. Ser.* 217, 1–14.
- Boehlert, G.W., 1988a. Current-topography interactions at mid-ocean seamounts and the impact on pelagic ecosystems. Proceedings, First Pacific Symposium on Marine Sciences, Nakhodka, USSR. *GeoJournal*, 16, 45–52.
- Boehlert, G.W., 1988b. Seamount acoustic scattering. *Eos, Trans.-Am. Geophys. Union* 69, 1619–1628.
- Boehlert, G.W., Genin, A., 1987. A review of the effects of seamounts on biological processes. In: Keating, B., Fryer, P., Batiza, R., Boehlert, G. (Eds.), *Seamounts, Islands and Atolls*. Geophysical Monograph, vol. 47. American Geophysical Union, Washington, DC, pp. 319–334.
- Boehlert, G.W., Wilson, C.D., Mizuno, K., 1994. Populations of the sternoptichid fish, *Maurolicus muelleri* on seamounts in the central North Pacific. *Pac. Sci.* 48, 57–69.
- Borkin, I.V., Grigorev, G.V., 1987. On the discovery of a marvolik, *Maurolicus muelleri*, along Novaya Zemlya. *J. Ichthyol.* 27, 139–141.
- Brainard, R.E., 1986. Fisheries aspects of seamounts and Taylor Columns. MS thesis, Naval Postgraduate School, Monterey, CA.
- Bray, R.N., 1981. Influence of water currents and zooplankton densities on daily foraging movements of blacksmith, *Chromis punctipinnis*, a planktivorous reef fish. *Fish. Bull. U.S.* 78, 829–841.
- Butman, B., Beardsley, R.C., 1987. Long-term observations on the southern flank of Georges Bank: Part 1. A description of the seasonal cycle of currents, temperature, stratification, and wind stress. *J. Phys. Oceanogr.* 17, 367–384.
- Clarke, W.D., 1962. The genus *Gnathophausia* (Mysidacea, Crustacea), its systematics and distribution in the Pacific Ocean. PhD dissertation, University of California.
- Clarke, T.A., 1973. Some aspects of the ecology of lanternfishes (Myctophidae) in the Pacific Ocean near Hawaii. *Fish. Bull. U.S.* 71, 401–434.
- Clarke, T.A., 1982. Distribution, growth, and reproduction of the lightfish *Maurolicus muelleri* (Sternoptichidae) off South-East Australia. Rep.-CSIRO Mar. Lab. 145.
- Comeau, L.A., Vezina, A.F., Bourgeois, M., Juniper, S.K., 1995. Relationship between phytoplankton production and the physical structure of the water column near Cobb Seamount, northeast Pacific. *Deep-Sea Res., Part 1, Oceanogr. Res. Pap.* 42, 993–1005.
- Dalpadado, P., Gjosaeter, J., 1987a. Observations on mesopelagic fish from the Red Sea. *Mar. Biol.* 96, 173–183.
- Dalpadado, P., Gjosaeter, J., 1987b. Feeding ecology of the lanternfish *Benthosema pterotum* from the Indian Ocean. *Mar. Biol.* 99, 555–567.
- de Forges, B.R., Koslow, J.A., Poore, G.C.B., 2000. Diversity and endemism of the benthic seamount fauna in the southwest Pacific. *Nature* 405 (6789), 944–947.
- Dower, J.F., Perry, R.L., 2001. High abundance of larval rockfish over Cobb Seamount, an isolated seamount in the Northeast Pacific. *Fish. Oceanogr.* 10, 268–274.
- Dower, J., Freeland, H., Juniper, K., 1992. A strong biological response to oceanic flow past Cobb Seamount. *Deep-Sea Res., A, Oceanogr. Res. Pap.* 39, 1139–1145.
- Fonteneau, A., 1991. Monts sous-marins et thons dans l'Atlantique tropical est. *Aquat. Living Resour.* 4, 13–25.
- Foote, K.G., Everson, I., Watkins, J.L., Bone, D.G., 1990. Target strengths of Antarctic krill (*Euphausia superba*) at 38 and 120 kHz. *J. Acoust. Soc. Am.* 87, 16–24.
- Genin, A., Boehlert, G.W., 1985. Dynamics of temperature and chlorophyll structures above a seamount: an oceanic experiment. *J. Mar. Res.* 43, 907–924.

- Genin, A., Dayton, P.K., Lonsdale, P.F., Spiess, F.N., 1986. Corals on seamount peaks provide evidence of current acceleration over deep-sea topography. *Nature* 322, 59–61.
- Gjosæter, J., 1981. Life history and ecology of *Maurolicus muelleri* (Gonostomatidae) in Norwegian waters. *Fisk. Dir. Skr., Ser. Hav. Unders.* 17, 109–131.
- Gjosæter, J., Kawaguchi, K., 1980. A review of the world resources of mesopelagic fish. Food and Agriculture Organization of the United Nations. FAO Fisheries Technical Paper No 193.
- Greenlaw, C.F., Percy, W.G., 1985. Acoustical patchiness of mesopelagic micronekton. *J. Mar. Res.* 43, 163–178.
- Hamano, A., Uchida, K., 1992. Target strength measurement of sternoptychid fish, *Maurolicus muelleri*, using 88 kHz quantitative echo sounder. *Bull. Japan. Soc. Fish. Ocean.* 56, 283–293.
- Hardy, A.C., 1956. The Open Sea. Its Natural History: The World of Plankton. Collins, London.
- Haurly, L.R., 1988. Vertical distribution of *Pleuromamma* (Copepoda: Metridinidae) across the eastern North Pacific Ocean. *Hydrobiologia* 167, 335–342.
- Hobson, E.S., Chess, J.R., 1976. Trophic interactions among fishes and zooplankters near shore at Santa Catalina Island, California. *Fish. Bull. U.S.* 74, 567–598.
- Isaacs, J.D., Schwartzlose, R.A., 1965. Migrant sound scatterers: interactions with the sea floor. *Science* 150, 1810–1813.
- Johannesson, K.A., Mitson, R.B., 1983. Fisheries acoustics. A practical manual for aquatic biomass estimation. FAO Fisheries Technical Paper. 240.
- Kalinowski, J., Linkowski, T.B., 1983. Hydroacoustic observations on *Maurolicus muelleri* (Sternoptychidae) over R.S.A. and discovery seamounts. *Coop. Res. Rep.-Int. Coun. Explor. Sea*, pp. 1–20. (ICES-CM-1983/H:16).
- Kaartvedt, S., 1989. Retention of vertically migrating suprabenthic mysids in fjords. *Mar. Ecol., Prog. Ser.* 57, 119–128.
- Kingsford, M.J., MacDiarmid, A.B., 1988. Interrelations between planktivorous reef fish and zooplankton in temperate waters. *Mar. Ecol., Prog. Ser.* 48, 103–117.
- Liljebladh, B., Thomasson, M.A., 2001. Krill behavior as recorded by acoustic Doppler current profilers in the Gullmarsfjord. *J. Mar. Syst.* 27, 301–333.
- Linkowski, T.B., 1983. Some aspects of the biology of *Maurolicus muelleri* (Sternoptychidae) from the South Atlantic. *Coop. Res. Rep.-Int. Coun. Explor. Sea*, pp. 1–21. (ICES-CM-1983/H:17).
- Loder, J.W., Ross, C.K., Smith, P.C., 1988. A space- and time-scale characterization of circulation and mixing over submarine banks, with application to the northwestern Atlantic continental shelf. *Can. J. Fish. Aquat. Sci.* 45, 1860–1885.
- Loeb, V.J., 1979. Vertical distribution and development of larval fishes in the North Pacific central gyre during summer. *Fish. Bull. U.S.* 77, 777–793.
- MacLennan, D.N., Simmonds, E.J., 1992. Fisheries Acoustics. Chapman and Hall, New York.
- McFarland, W.N., Kotchian, N.M., 1982. Interaction between schools of fish and mysids. *Behav. Ecol. Sociobiol.* 11, 71–76.
- Mukhacheva, V.A., 1981. Geographical distribution and variability of *Maurolicus muelleri* (Gmelin) (Sternoptychidae, Osteichthys). In: *Fishes of the Open Ocean*. Institute of Oceanology, Acad. of Sci. USSR, pp. 41–46.
- Mullineaux, L.S., Mills, S.W., 1997. A test of the larval retention hypothesis in seamount-generated flows. *Deep-Sea Res.* 44, 745–770.
- Neilson, J.D., Perry, R.I., 1990. Diel vertical migrations of marine fishes: an obligate or facultative process? *Adv. Mar. Biol.* 26, 115–168.
- Nero, R.W., Magnuson, J.J., 1989. Characterization of patches along transects using high-resolution 70-kHz integrated acoustic data. *Can. J. Fish. Aquat. Sci.* 46, 2056–2064.
- Noble, M., Mullineaux, L.S., 1989. Internal tidal currents over the summit of Cross Seamount. *Deep-Sea Res.* 36, 1791–1802.
- Okiyama, M., 1971. Early life history of the gonostomatid fish, *Maurolicus muelleri* (Gmelin), in the Japan Sea. *Bull. Jpn. Sea Reg. Fish. Res. Lab.* 23, 21–53.
- Owens, W.B., Hogg, N.G., 1980. Oceanic observations of stratified Taylor Columns near a bump. *Deep-Sea Res.* 27A, 1029–1045.
- Parin, N.V., 1986. Distribution of mesobenthopelagic fishes in slope waters and around submarine rises. UNESCO Tech. Pap. Mar. Sci. 49, 226–229.
- Parker, T., Tunncliffe, V., 1994. Dispersal strategies of the biota on an oceanic seamount: implications for ecology and biogeography. *Biol. Bull.* 187, 336–345.
- Percy, W.G., 1970. Vertical migration of the ocean shrimp, *Pandalus jordani*: a feeding and dispersal mechanism. *Calif. Fish Game* 56, 125–129.
- Percy, W.G., Krygier, E.E., Mesecar, R., Ramsey, F., 1977. Vertical distribution and migration of oceanic micronekton off Oregon. *Deep-Sea Res.* 24, 223–245.
- Pearre, S., 1979. Problems of detection and interpretation of vertical migration. *J. Plankton Res.* 1, 29–44.
- Pereyra, W.T., Percy, W.G., Carvey Jr., F.E. 1969. *Sebastes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. *Can. J. Fish. Aquat. Sci.* 26, 2211–2215.
- Peterson, W., 1998. Life cycle strategies of copepods in coastal upwelling zones. *J. Mar. Syst.* 15, 313–326.
- Raugust, S.C., Brainard, R.E., Garwood, R.W., 1988. Bottom moored current meter data from the Southeast Hancock Seamount in April, 1987. Naval Postgraduate School, Monterey CA 93943-5000. NPS 68-88-008.
- Reid, S.B., Hirota, J., Young, R.E., Hallacher, L.E., 1991. Mesopelagic-boundary community in Hawaii: micronekton at the interface between neritic and oceanic ecosystems. *Mar. Biol.* 109, 427–440.
- Robertson, A., Powers, C.F., Anderson, R.F., 1968. Direct observations on *Mysis relicta* from a submarine. *Limnol. Oceanogr.* 13, 700–702.
- Roden, G.I., 1987. Effect of seamounts and seamount chains on ocean circulation and thermohaline structure. In: Keating, B.H., Fryer, P., Batiza, R., Boehlert, G.W. (Eds.), *Seamounts, Islands and Atolls*. Geophys. Monogr. vol. 43. American Geophysical Union, Washington, DC, pp. 335–354.
- Roden, G.I., Taft, B.A., Ebbesmeyer, C.C., 1982. Oceanographic aspects of the Emperor Seamounts region. *J. Geophys. Res.* 87, 9537–9552.
- Saltzman, J., Wishner, K.F., 1997. Zooplankton ecology in the eastern tropical Pacific oxygen minimum zone above a sea-

- mount: 1. General trends. Deep-Sea Res., Part 1, Oceanogr. Res. Pap. 44, 907–930.
- Sassa, C., Kawaguchi, K., Kinoshita, T., Watanabe, C., 2002. Assemblages of vertical migratory mesopelagic fish in the transitional region of the western North Pacific. Fish. Oceanogr. 11, 193–204.
- Shomura, R.S., Barkley, R.A., 1980. Ecosystem dynamics of seamounts—a working hypothesis. Proc. 4th Symp. Co-Op. Study of the Kuroshio and Adjacent Regions. Saikon Publ., Tokyo, pp. 789–790.
- Sponaugle, S., Cowen, R.K., Shanks, A., Morgan, S.G., Leis, J.M., Pineda, J., Boehlert, G.W., Kingsford, M.J., Lindeman, K., Grimes, C., Munro, J.L., 2002. Predicting self-recruitment in marine populations: biophysical correlates. Bull. Mar. Sci. 70 (Supplement), 341–375.
- Torgersen, T., Kaartvedt, S., Melle, W., Knutsen, T., 1997. Large scale distribution of acoustical scattering layers at the Norwegian continental shelf and the eastern Norwegian Sea. Sarsia 82, 87–96.
- Tseytlin, V.B., 1985. Energetics of fish populations inhabiting seamounts. Oceanology 25, 237–239.
- Uchida, R.N., Tagami, D.T., 1984. Groundfish fisheries and research in the vicinity of seamounts in the North Pacific Ocean. Mar. Fish. Rev. 46, 1–17.
- Uchida, R.N., Hayasi, S., Boehlert, G.W., eds., 1986. Environment and resources of seamounts in the North Pacific. NOAA Tech. Rep., NMFS 43.
- Vereshchaka, A.L., 1995. Macroplankton in the near-bottom layer of continental slopes and seamounts. Deep-Sea Res., Part 1, Oceanogr. Res. Pap. 42, 1639–1668.
- Wilson, C.D., 1992. Interactions of ocean currents and diel migrators at a seamount in the central North Pacific. PhD dissertation, University of Hawaii. Honolulu, HI.
- Wilson, C.D., Boehlert, G.W., 1990. Acoustic measurement of micronekton distribution over Southeast Hancock Seamount, Central Pacific Ocean. In: Singal, S.P. (Ed.), Acoustic Remote Sensing: Proceedings of the Fifth International Symposium on Acoustic Remote Sensing of the Atmosphere and Oceans. McGraw-Hill, New Delhi, pp. 222–229.
- Wilson, C.D., Boehlert, G.W., 1993. Population biology of *Gnathophausia longispina* (Mysidacea, Lophogastrida) from a central North Pacific Seamount. Mar. Biol. 115, 537–543.
- Wilson, C.D., Firing, E., 1992. Sunrise swimmers bias acoustic Doppler current profiles. Deep-Sea Res., Part 1, Oceanogr. Res. Pap. 39, 885–892.
- Wooldridge, T., Erasmus, T., 1980. Utilization of tidal currents by estuarine zooplankton. Estuar. Coast. Shelf Sci. 11, 107–114.
- Young, J.W., Blaber, S.J.M., 1986. Feeding ecology of three species of midwater fishes associated with the continental slope of eastern Tasmania, Australia. Mar. Biol. 93, 147–156.
- Zar, J.H., 1984. Biostatistical Analysis. Prentice-Hall, Englewood Cliffs, NJ.