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Current-Topography Interactions at Mid-Ocean Seamounts and the Impact on Pelagic Ecosystems

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ABSTRACT: Ocean currents impinging on topographic obstacles such as seamounts create a high level of variability in mesoscale physical oceanography. In the N Pacific, for example, the structure of the Kuroshio and its extension differ significantly E and W of the Emperor Seamount chain, and eddy fields detected downstream may be attributed to seamount effects. Nearfield effects of seamounts have been theoretically predicted for several decades but only recently has theory been confirmed by observation. Taylor columns, quasi-stationary eddies over seamounts, alter flow patterns and thus have impacts on both benthos on seamounts and on the biota in water overlying the seamount.

SE Hancock Seamount, located at the N end of the Hawaiian Ridge (29°47'N; 179°04'E), has a summit depth of 265 m. This seamount is located near the subtropical front and is at the southerly extent of productive seamounts where trawl fisheries have existed in the past. The pelagic ecosystem in the upper 200 m over the seamount clearly differs from waters at control stations at distances of 10's of kilometers away as shown by plankton and midwater trawl hauls and hydroacoustic transects conducted during 1984 and 1985. Over the seamount, hydroacoustic transects show a significantly higher biomass of scatterers as compared to control stations. Sampling these scattering layers with small midwater trawls demonstrates high densities of a resident micronekton fauna dominated by the sternoptychid fish "Maurolicus muelleri" and the mysid "Gnathophausia longispina"; these taxa were virtually absent from the control stations, were oceanic micronekton, particularly larger forms, were generally in higher abundance than at the seamount stations. Similarly, ichthyoplankton abundance differs above the seamount and at reference stations. In summer sampling, larval fishes were less abundant over the seamount whereas in winter the abundance was greater there. The differences in distribution and abundance of both micronekton and ichthyoplankton are significant and consistently observed, suggesting that physical or biological processes at the seamount have important effects on the pelagic ecosystem. Hypotheses concerning current - topography interactions, exclusion of vertical migrators, and predation by resident micronekton and fishes can be used to explain the observed effects.

Seamounts and other areas of complex topography are frequently sites of highly productive ecosystems; the S Emperor and N Hawaiian Ridge seamounts provide a good example, with a catch of approximately one million tons of boarfish in ten years. The interaction of ocean currents and complex topography may play an important role in this high productivity, as demonstrated in the high biomass of lower trophic levels in the seamount ecosystem. Interannual variability in the latitudinal position of the subtropical front and the strength of current flow over these seamounts may result in significant differences in mesoscale physical oceanography and therefore in the productivity of these ecosystems.

Introduction

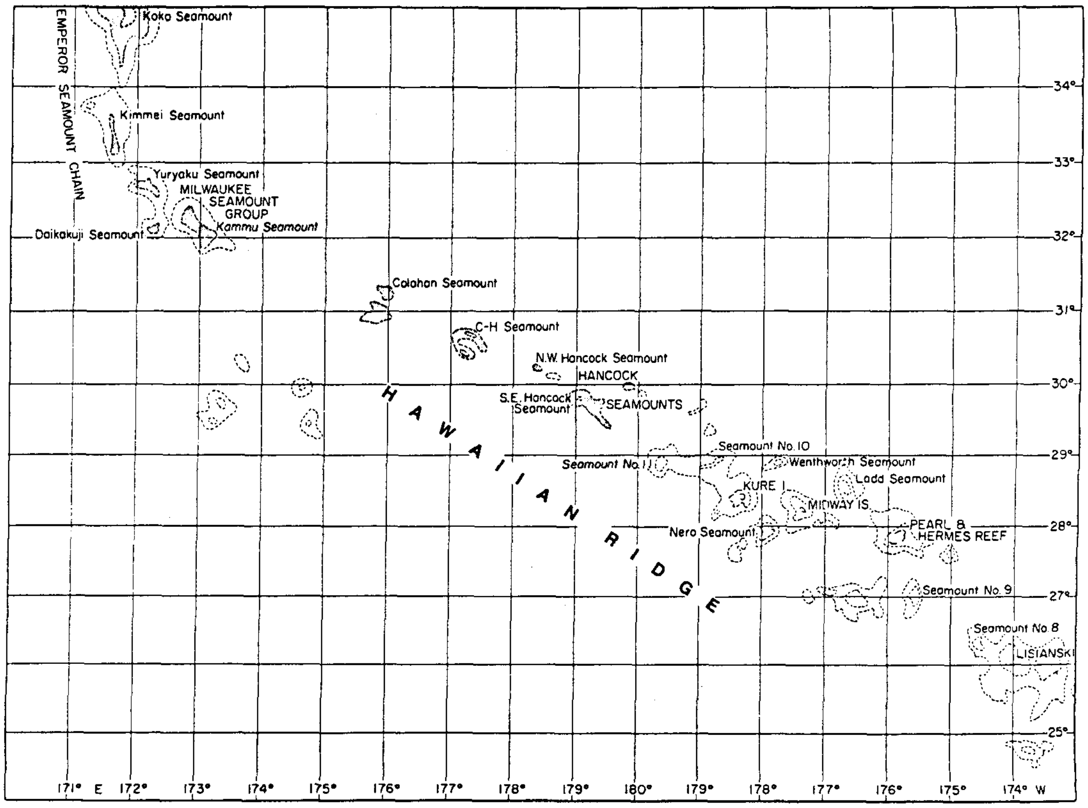
In the open ocean, seamounts interact with ocean currents to create considerable variability in the physical flow field. Several studies have described these effects on the Gulf Stream (Vastano and Warren 1976; Hurlburt and Thompson 1984) and the Kuroshio (Roden et al. 1982; Roden 1986; Darnitsky 1980b; Kozlov et al. 1982). The physical effects may spawn mesoscale eddies which alter flow patterns for significant distances downstream of the seamounts (Royer 1978). Biological effects of these physical complexities are not well understood (Boehlert 1986). Discovery of seamount fishery (Uda and Ishino 1958; Borets 1975) and mineral resources (Manheim 1986), however, has caused increased interest in seamount oceanography and its effects on biota (Bezrukov and Natarov

1976; Darnitsky et al. 1984; Genin and Boehlert 1985; Uchida et al. 1986).

The effect of sea floor topography on ocean currents has been a topic of interest to physical oceanographers for several decades. This area has recently been reviewed by Hogg (1980) and was the topic of a monograph by Kozlov (1983). Taylor columns, semistationary eddies located above seamounts, have been theoretically predicted and experimentally demonstrated for several decades (Taylor 1917; Huppert and Bryan 1976); they have been observed over some seamounts (Darnitsky 1980b; Owens and Hogg 1980; Richardson 1980). Taylor columns are likely generated over central N Pacific seamounts, where eddies have been observed (Cheney et al. 1980; Darnitsky 1980a); unfortunately oceanographic surveys generally have station patterns inappropriate to detect these open-ocean small-scale or mesoscale phenomena (Roden 1986). Still, past theoretical and observational studies on the physics of topographic effects are available to serve as a background for biological studies.

Many studies have suggested that ecosystems at banks or seamounts are highly productive (Uda and Ishino 1958; Fedosova 1974; Bezrukov and Natarov 1976; Zaika and Kovalev 1984; Tseitlin 1985). The ideas which explain such high productivity are typically based upon either local enhancement and subsequent retention of productivity or advection and concentration of food produced elsewhere. Some support exists for each of these hypotheses. Differences often exist between the pelagic ecosystems of waters above seamounts and adjacent, oceanic waters, including plankton biomass (Bezrukov and Natarov 1976), ichthyoplankton (Nellen 1973), and chlorophyll (Genin and Boehlert 1985). In the case of advected productivity, however, seamount populations may not be limited by local production, but rather by physical aggregation mechanisms (Isaacs and Schwartzlose 1965; Darnitsky et al. 1984), which have been

Fig 1 **The S Emperor - N Hawaiian Ridge seamounts. Current flow in this region is dominated by easterly flow from the Kuroshio N of the subtropical front, but this front can vary seasonally (and interannually) between lat. 28° and 32°N (Roden 1970); S of the front, westerly flow may be observed.**



shown to exist in a variety of situations (Alldredge and Hamner 1980; Olson and Backus 1985). In the present paper I describe the effects of an open-ocean seamount on the distribution and abundance of planktonic and micronektonic organisms.

Materials and Methods

Sampling was conducted at the Hancock Seamounts in the central N Pacific, some 180 nmi NW of Kure Atoll, the nearest emergent land (Fig 1). Each of the two seamounts on this large bank (Southeast Hancock, lat. 29°48'N, long. 178°05'E; Northwest Hancock, lat. 30°17'N, long. 178°44'E) rise to within approximately 265 m of the surface from a background bottom depth of nearly 5 km. Samples described in this study were taken during two cruises of the NOAA ship *Townsend Cromwell* to these seamounts in July-August 1984 and January-February 1985.

A variety of physical measurements were made during these cruises (Brainard and Wittman 1985), but for the purposes of this paper, only thermal structure and summer surface currents will be described. Temperature profiles were taken with expendable bathythermographs (XBT, T-4, Sippican Corp.), which record to 450 m, well below the depth of the seamount summit. Surface bucket thermometer observations were made to check on the XBT readings at the surface. On the summer 1984 cruise, surface currents were estimated with 13 radio-tracked Lagrangian drifters drogued at a depth of 10 m.

Biological sampling was conducted with several gear types. The behavior of seamount-associated scattering layers was observed with a 38 kHz Simrad echo sounder and a Raytheon-JRC chromoscope configured as a slave indicator for the Simrad. Micronekton samples from the scattering layers were taken with a 1.8 m Isaacs-Kidd midwater trawl (IKMT) fitted with a calibrated General Oceanics flowmeter to estimate volume filtered. Appropriate mesh sizes were used to minimize extrusion of the taxa considered in this report. Tows with the IKMT were taken above both SE and NW Hancock Seamounts; comparison tows were taken at reference stations ranging from 2 to 20 km from the summit to determine the composition and abundance of micronekton in oceanic waters. All IKMT hauls were taken at night. Hauls over the seamount were typically targeted to fish within scattering layers; hauls away from the seamount targeted scattering layers if they were evident or were fished at the same depths as those over the seamount if they were not.

Ichthyoplankton samples were taken with a three-net Tucker trawl with a messenger-actuated closing device in the manner described by Boehlert et al. (1985). All nets taking samples were equipped with calibrated flowmeters. Duplicate

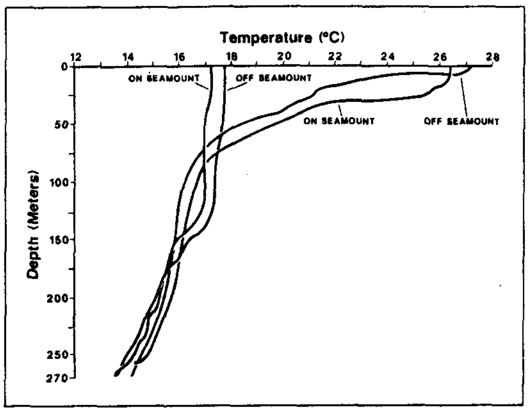
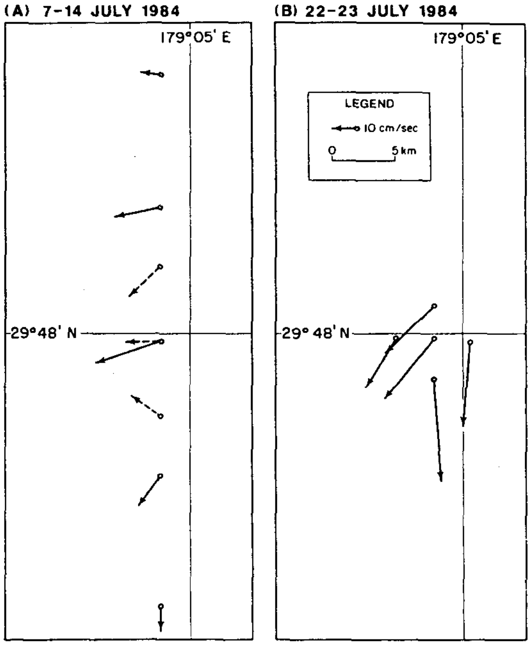


Fig 2 Temperature-depth profiles taken at SW Hancock Seamount in summer 1984 (warm surface temperatures) and winter 1985. The "on seamount" profiles were taken near the center of the seamount summit, the "off seamount" profiles at a reference station some 20 km distant from the summit.

Fig 3 Surface current patterns at SE Hancock Seamount for two periods during summer 1984. Magnitude of current speed is indicated by the length of the arrows. These data are based upon radio-tracked Lagrangian drifters drogued at 10 m for periods ranging from 10 to 41 hours. Although the drift trajectories were calculated over several intervening periods, the direction shown is based upon the starting and ending positions. The location of the seamount summit is indicated by the intersection of the two lines.


(A) 7-14 JULY 1984

(B) 22-23 JULY 1984

samples were taken as stepped oblique tows within discrete depth zones of 0-25, 25-50, 50-100, and 100-200 m both day and night. Seamount hauls were made over the summit of SE Hancock Seamount, while the reference station was 20 km west of the seamount summit. All biological samples were immediately preserved in 10% Formalin in seawater buffered with sodium borate. In the laboratory, specimens were sorted from the entire volume of each sample.

Results

The physical environment differed between summer and winter at these seamounts, as has been described generally by Fedosova (1974) and Darnitsky et al. (1984). Surface temperatures were generally between 26° and 28°C in the summer and 17° and 18°C in winter (Fig 2). A strong thermocline was present near 70 m in summer but the surface waters were well mixed to 120 m or more in winter. A comparison of the thermal structure above the seamounts and at reference stations shows differences between summer and winter. Although these XBT casts were not taken synoptically, they are representative of the temperature patterns observed in many XBT casts. In summer, the temperature above the seamount was typically warmer than at corresponding depths at the reference station; the reverse was true in winter (Fig 2).

Current patterns in summer 1984 were estimated from 13 drogues released on three different dates. Surface currents ranged from 9 to 42 cm/sec and were westward in the first set but directed more southward in the second set (Fig 3).

Hydroacoustic observations on both summer and winter cruises were generally taken from early evening to morning to observe the behavior of seamount-associated scattering layers. Scattering layers were better developed during the summer cruise and were most consistent from night to night as compared to winter; they will thus be discussed in most detail here. During daylight hours, scatterers were distinct on the flanks of the SE Hancock Seamount at depths of approximately 400 m. As dusk approached, the scatterers began streaming vertically upward to depths near 50 m (Fig 4A). This was followed by consolidation of the shallow layers, a slight sinking of the top layer, and expansion downwards until the scattering layer extended from the summit of the seamount upwards to approximately 100 m depth (Fig 4B). The layer remained relatively stationary and coherent throughout the night; as light intensity increased the following morning, some scatterers dispersed upwards, reaching near-surface waters (Fig 4C). As the sun came over the horizon, these shallow layers consolidated and moved rapidly downward. Some scatterers remained in the water column above the seamount flanks later in the morning, present at depths as shallow as 170 m (Fig 4D). No deep scattering layers in surrounding

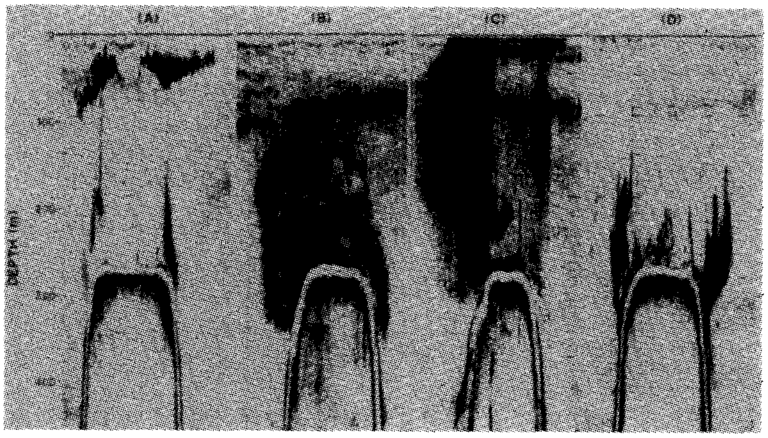


Fig 4
Time series of acoustic transects over SE Hancock Seamount on 17-18 July 1984 showing behavior of the scatterers. Each transect, from W to E (left to right) near the central axis of the seamount, took approximately 25 minutes. The distance across the flat portion of the seamount is approximately 1.8 km.

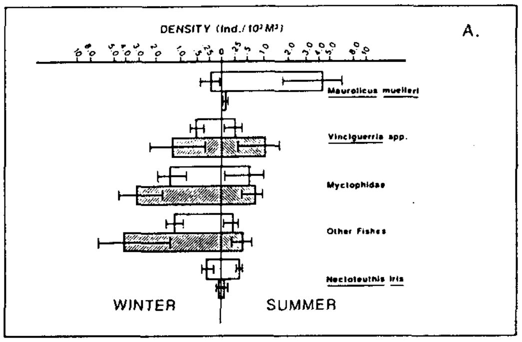
A. 1931 h. Note the scattering layers rising off the seamount flanks to a depth of 40-60 m; net samples show these early layers to be predominantly "Maurolicus muelleri". Sunset was at 1970 h.
B. The layer has developed around the seamount extending from the flanks upwards to near 100 m; it developed this configuration at approximately 2130 h and remained similar throughout the night. This transect was at 0330 h.
C. 0430 h. As light intensity increased, the layer dispersed and moved rapidly upward. As the sun came over the horizon at 0515 h, however, the layer consolidated and moved rapidly downward.
D. 0630 h. The scattering layers remained high in the water column above the flanks later into the morning. These scattering targets may have been larger fishes or squids not sampled by our midwater trawl.

oceanic waters displayed either such high density or this type of behavior, suggesting that organisms specific to the region of the seamount were responsible for the acoustic traces.

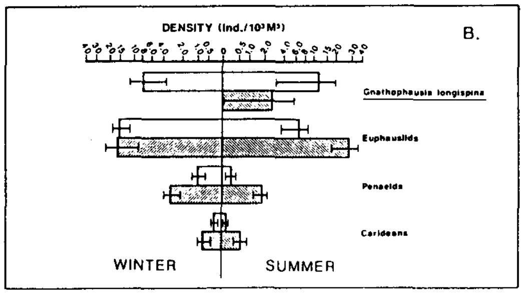
Micronekton samples from the IKMT were generally different between waters above the seamount and at the reference stations. In the summer samples (Fig 5) the sternoptychid fish, *Maurolicus muelleri*, and the lophogastrid mysid, *Gnathophausia longispina*, dominated the catch over the seamounts. A third species, the sepiolid squid, *Nectoteuthis (Iridioteuthis) iris*, was characteristic of the deeper portions of the seamount scattering layer. Early evening IKMT hauls through the scattering layer in shallow water (Fig 4A) were typically dominated by *M. muelleri* with very few crustaceans; later samples included larger catches of *G. longispina* and euphausiids. Since the net was open at all times, samples taken above the seamount were only in the scattering layers for about 50% of the sampling time; thus the estimates of the seamount-associated micronekton are minimum values.

Micronekton samples taken at the reference stations differed in both abundance and composition as compared to seamount samples. Oceanic taxa were generally more abundant, suggesting that the oceanic ecosystem is affected by the seamount or its biota. The three seamount taxa were either absent or in low abundance. The photichthyid fish *Vinciguerria attenuata* and *V. nimbaria* were more abundant in waters away from the seamount, while densities of myctophids and all other fishes combined were not significantly different (Fig 5A). All oceanic crustacean groups, however, were significantly more abundant in tows away from the seamount (Fig 5B). In winter months, most of the same taxa were present, with similar relationships between on- and off-seamount hauls; the exception to this statement is the very low abundance of *M. muelleri* over the seamounts (Fig 5A) and higher relative densities of euphausiids above the seamount (Fig 5B).

Ichthyoplankton densities from the summer cruise taken in daytime showed no difference between samples over the seamount and those at the reference station with the exception of the 50-100 m stratum (Fig 6A). At night, however, the densities at the reference station were significantly increased as compared to daytime values, but there was no corresponding density increase in the samples taken over the seamount. Thus at all depths, there were significantly fewer larvae present over the seamount than at the reference station. In these samples, shallow layers were dominated by the gonostomatid *Cyclothone* spp. and deeper ones (>50 m) by the myctophid *Diogenichthys atlanticus*. These relatively passive components of the plankton reflect the same pattern as the migrating micronekton (Figs 5A,B) during summer months. Samples taken on the winter cruise showed a different pattern from that in the summer (Fig 6B); ichthyoplankton densities over the seamount were much greater than at the reference station, and the pattern held for both night and day. While there were fewer *Cyclothone* in the samples, they were nonetheless dominated by midwater fish taxa as opposed to seamount-associated fishes.



Squids–Fishes



Crustacea

Fig 5 *Densities of selected micronekton taxa captured in* the Isaacs-Kidd midwater trawl samples.
A. Fishes and squid. - B. Crustacea.
In each panel, data from the summer 1984 cruise are on the right, winter 1985 on the left. In the summer cruise, data are from 12 hauls over the summit and 6 hauls at reference stations; the corresponding numbers for the winter cruise are 12 and 10, respectively. Two values are represented for each taxon; the upper (solid) bar indicates mean density (± 2 S.E.) from the tows over the seamount while the lower (cross-hatched) bar indicates mean densities in off-seamount tows.

Discussion

Seamounts and other complex topography may be the sites of aggregations of many animals, including tunas (Yasui 1986), marine mammals (Hiu 1985), and other organisms which apparently feed on prey aggregations found at physical discontinuities (Uda and Ishino 1958). There may also be relative enrichment of the benthos in such locations (Genin et al. 1986). Studies of sonic scat-

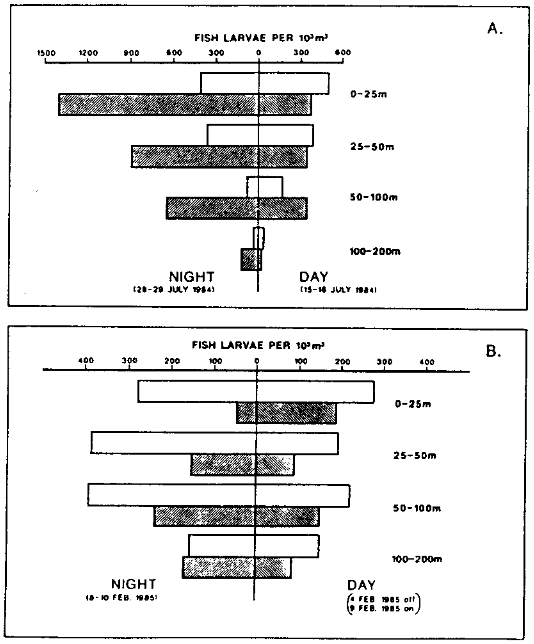


Fig 6 Ichthyoplankton densities near SE Hancock Seamount taken in Tucker trawl samples.
A. Summer 1984. - B. Winter 1985.
Daytime densities are on the right, nighttime on the left, with each value the mean of duplicate samples. Densities above the seamount are represented by the upper (solid) bar, densities at the reference station by the lower (cross-hatched) bar.

tering layers in wide ocean areas have demonstrated increased plankton or micronekton biomass near banks and islands (Hargreaves 1975); similarly, plankton biomass may increase around islands (Jones 1962). Few studies, however, have demonstrated the high densities of selected micronekton taxa observed over Hancock Seamount (Fig 5), suggesting that the presence of the seamount in some manner induces aggregation of these animals. Abundance of the three organisms we designate as seamount-associated micronekton *(M. muelleri, G. longispina,* and *N. iris)*, is unexpected in mid-ocean regions. *Maurolicus muelleri*, also known as the lightfish, is a cosmopolitan species often found in very high abundance but generally near continental shelf-slope break regions (Robertson 1976; Okiyama 1981); despite several midwater trawl surveys, it is not known from oceanic regions (Barnett 1984). Densities reported in this study are as high as 13.8 per 10^3 m^3 in summer and 1.2 per 10^3 m^3 in winter. *Gnathophausia longispina* is a shallow living member of this mysid genus and the only one which migrates vertically (Clarke 1962); it has been taken in the past only in small numbers but in this study, an average of 105 per positive tow in summer (with a maximum density of 42.7 per 10^3 m^3) and 78 in winter were taken. Finally, *N. iris* is a poorly known species which we have taken in previous bottom trawls on Hancock Seamounts; although present in our midwater trawls, it has been called a predominantly bottom-associated form, similar to other members of the subfamily Heteroteuthinae (Young 1978).

Densities of oceanic taxa of both micronekton (Fig 5) and fish larvae (Fig 6) above the seamount differ from that in adjacent waters, suggesting that they are in some way impacted by the seamount. Similar results with ichthyoplankton have been noted in the past, but the changed densities were typically neritic species (Nellen 1973). This phenomenon was not observed, however, over central N Pacific seamounts (Borets and Sokolovsky 1978) or in the Indian Ocean (Belyanina 1985). The generally lower abundance of oceanic taxa and population maintenance of the seamount-associated taxa can be explained by biological and physical mechanisms and I provide here three hypotheses which, in combination, may help explain the observed phenomena, as follows:

- current-topography interaction forms semistationary eddies or Taylor columns in the region of the seamount;
- the seamount serves to exclude upward vertical migrators from waters above the seamount;
- predation by resident fauna reduces abundance of oceanic species.

Taylor columns could be important both in maintaining planktonic or micronektonic populations and, through upwelling, could increase primary and secondary productivity (Genin and Boehlert 1985). From a theoretical standpoint, Taylor column formation is a function of current strength, seamount morphology, stratification of the water column, and latitude (Huppert 1975). Anticyclonic flow around the seamount should exist, with cold water at its center; warm water cyclonic eddies would remain in the vicinity of the seamount at low current speeds and are shed downstream at higher current speeds (Owens and Hogg 1980). Such a semistationary water column or eddy could maintain the observed community of seamount-associated micronekton. Surface currents over SE Hancock Seamount averaged 22.4 cm/sec (Fig 3) during our summer survey; it is unlikely that the small micronektonic *Gnathophausia* and *Maurolicus* could maintain their horizontal position at distances up to 190 m above seamount in such a current regime, but the scattering layers persisted throughout the night. It is also interesting that after the initial rise to shallower depths (Fig 4A), the top of the scattering layer appears truncated (Fig 4B) near the bottom of the mixed layer (Fig 2), suggesting that a trapped Taylor column (Dooley 1984), not reaching the surface, might be present. Theoretical calculations (Huppert 1975; Huppert and Bryan 1976) based upon the physical characteristics of SE Hancock Seamount and the observed summer current regime would predict the presence of a Taylor column.

The lower abundance of many of the oceanic micronekton in waters above the seamount (Fig 5) may be explained by exclusion of vertical migrators. The relative decrease in density of many of the oceanic crustaceans over the seamount seems to be related to size, which in turn may be related to the magnitude of vertical migration (Roger and Grandperrin 1976). This mechanism would likely interact with any stationary water column, however, since under uniform flow past the seamount, the water column would be completely replaced by advection after two to three hours, resulting in densities which should be similar to those of the reference stations.

The reduction in oceanic taxa, including ichthyoplankton, may also be related to predation. Many of the resident fishes of these seamounts, which may occur in high biomass, feed primarily upon oceanic micronekton and particularly on these larger crustaceans (Fedosova 1976; Humphreys and Tagami 1986). A predation-mediated reduction is also supported by the decreased nighttime densities of larval fishes over the seamount in summer (Fig 6A); these organisms are of the appropriate size spectrum for prey of *M. muelleri* (Hirota and Boehlert 1985), which has a very high biomass during that period (Fig 5). The lack of a difference in summer daytime densities, moreover, is consistent with the absence of *M. muelleri* from the water column during the day (Fig 4). The low abundance of *M. muelleri* in winter months may result in reduced predation on ichthyoplankton but cannot explain the higher abundance above the seamount (Fig 6B).

The observed patterns of micronekton and ichthyoplankton distributions may be based upon a combination of the hypotheses described above. The maintenance of high densities of seamount-associated micronekton over seamounts, however, must require a large forage base. In turn, these micronektonic species probably served as a part of the forage base for higher trophic levels. An important fishery existed on Hancock and several of the S Emperor Seamounts; between 1967 and 1975, nearly one million metric tons of pelagic armorhead, *Pseudopentaceros wheeleri*, were taken from these seamounts by Soviet and Japanese trawlers, and standing stocks of nearly 400,000 metric tons were estimated (Borets 1975; Sasaki 1986). Some of the same physical mechanisms which alter the patterns of distribution and abundance of the taxa as described in this paper may be invoked to explain the availability of the energy necessary to maintain high densities of fish. First, convergent flow resulting in accumulation of the background oceanic plankton and micronekton may provide prey (Isaacs and Schwartzlose 1965; Darnitsky et al. 1984; Tseitlin 1985). Secondly, upwelling associated with flow around topography may increase nutrients and biological productivity in surface waters (Uda and Ishino 1958; Genin and Boehlert 1985); in this case, however, there must be some mechanism by which this productivity is retained in the region of the seamount. A Taylor column or other stationary water mass could retain this productivity, but the residence times of such features are unknown.

It is clear from these results that seamounts induce biological variability in mid-ocean pelagic ecosystems. Above this seamount I observed depletion of some organisms and abundance of others (Fig 4, 5, 6). Interacting with oceanic currents, seamounts apparently generate and shed mesoscale eddies which are detectable downstream (Royer 1978). Eddies may maintain their integrity with respect to physical and biological characteristics for long periods (Ortner et al. 1978; Owen 1981; Olson and Backus 1985; Wiebe et al. 1985). Thus eggs, larvae, and even adults of seamount-associated species may occur in isolated eddies distant from the seamounts, which could similarly be depleted in oceanic species. Since current speed plays such an important role in the physical dynamics of these systems (Huppert and Bryan 1976; Kozlov 1983), interannual variability in the magnitude and direction of ocean currents can have strong effects on the productivity of these ecosystems. Interannual variability in the latitudinal position of the subtropical front, which will exert strong effects in the region of the Hancock Seamounts (Fig 1) is well known (Roden 1970). Similarly, interannual variability in eddy production has been observed in the Kuroshio system (Mizuno and White 1983). Further understanding of the interaction of currents with mid-ocean seamounts will be necessary to understand the dynamics of these unique ecosystems.

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