A REVIEW OF THE EFFECTS OF SEAMOUNTS ON BIOLOGICAL PROCESSES

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Abstract. Seamounts interacting with oceanic currents create flow complexities which depend upon current speed, stratification, latitude, and seamount morphology. Seamount effects, which include internal wave generation, eddy formation, local upwelling, and closed circulation patterns called Taylor columns, have important effects upon pelagic and benthic ecosystems over seamounts. The biological effects of these current-topography interactions are poorly understood. Flow acceleration on upper flanks of seamounts may lead to low sedimentation but areas of high standing stocks of benthic fauna, particularly filter feeders. Other effects extend into the water column; nutrient enrichment and enhanced primary productivity occur over some seamounts. Longer observational periods will be necessary to understand the time-varying nature of such enhanced productivity and the extent to which it remains at the seamount or is advected away. At higher trophic levels, unusual patterns of distribution and abundance occur at some seamounts. Maintenance of high standing stocks of seamount-associated micronekton and demersal fishes suggests that seamounts are locations for high rates of energy transfer. The energy driving this biological productivity may either be generated from in situ processes or be advected from elsewhere and concentrated at the seamount; interdisciplinary studies will be necessary to better understand these ecosystems.

Introduction

Seamounts represent a major physical feature of all ocean basins. For marine biota, they may be considered as islands separated by deep ocean areas; seamounts were thus the topic of many biogeographic studies [Wilson and Kaufman, 1987]. Biological communities at seamounts, however, may differ qualitatively and quantitatively from their continental shelf or slope counterparts at similar water depths [Hubbs, 1959]. In the open ocean, seamounts interact with ocean currents and create variability in the physical flow field. Several studies have described these effects on the Gulf Stream [Vastano and Warren, 1976] and the Kuroshio [Roden et al., 1982; Roden, 1987]. The physical effects include local small- and mesoscale phenomena including the shedding of 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 [Genin and Boehlert 1985; Boehlert, 1986]. Discovery of seamount fishery [Uchida and Tagami, 1984] and mineral resources [Manheim, 1986], however, has caused increased interest in seamount oceanography and its effects on biota [Darnitsky et al., 1984; Genin and Boehlert, 1985; Uchida et al., 1986].

The effects of sea floor topography on ocean currents have 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]. Semistationary eddies or Taylor columns above seamounts have been theoretically predicted and experimentally demonstrated in the laboratory [Taylor, 1917; Huppert and Bryan, 1976] and have been observed over scme seamounts [Darnitsky, 1980; Owens and Hogg, 1980; Richardson, 1980]. Unfortunately, oceanographic surveys generally have station patterns inappropriate to detect these openocean, 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 certain banks or seamounts are highly productive [Uda and Ishino 1958; Fedosova, 1974; Zaika and Kovalev, 1984; Tseitlin, 1985]. The ideas which explain such high productivity are typically based upon either local enhancement and subsequent
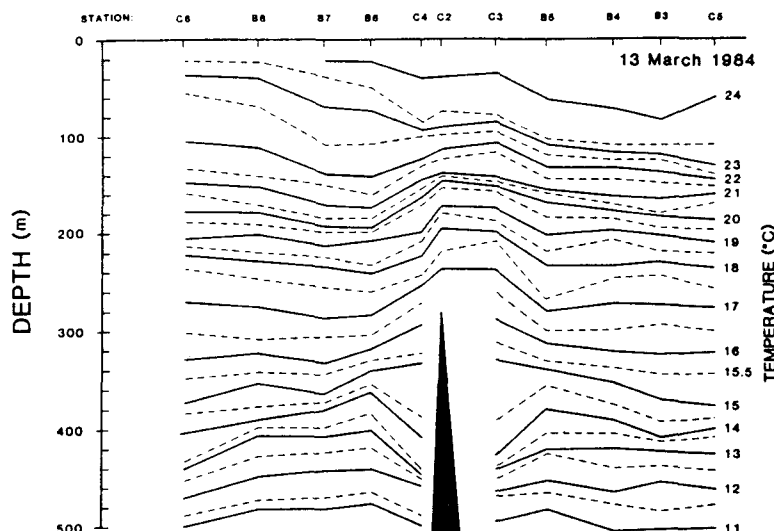
Fig. 1. Temperature structure at Minami-Kasuga Seamount (lat. 21°6'N, long. 143°8'E) along a west-east transect showing uplifted isotherms over the summit of the seamount. Note that the vertical scale is 50 times greater than the horizontal scale. (From Genin and Boehlert, 1985.)

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 nutrient concentrations [Kozlov et al., 1982], chlorophyll [Genin and Boehlert, 1985], plankton biomass [Bezrukov and Natarov, 1976], ichthyoplankton [Nellen, 1973], and micronekton [Boehlert and Seki, 1984]. 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 shown to exist in gyres and near reefs and coastal headlands [Alldredge and Hamner, 1980; Olson and Backus, 1985]. Benthic ecosystems on seamounts and islands may similarly differ from corresponding systems on continental shelves and slopes but have typically been less well studied. In many cases, unusual or even unique faunas exist [Simpson and Heydorn, 1965; Littler et al., 1986]. In addition, more recent studies have investigated the relationship of benthic fauna to current speeds and seamount-induced physical variability [Genin et al., 1986]. In this paper we review the effects of seamounts on biological processes, particularly as they affect pelagic and benthic ecosystems and fisheries productivity.

The Pelagic Ecosystem at Seamounts

Much of the impact of seamounts on pelagic ecosystems may be traced to current-topography interactions, which have been summarized in this volume by Roden [1987]. Where seamounts act as obstacles to current flow, compression of streamlines will occur due to flow acceleration. Local deflections of isotherms, usually in the form of uplifting, have been observed above several seamounts at different locations and depths [Meincke, 1971; Vastano and Warren, 1976]. Taylor columns represent an interesting phenomenon pertinent to seamounts; associated theory [Taylor, 1923; Huppert and Bryan, 1976] predicts such deflections as a result of the encounter between a current and a seamount. Under certain conditions of current, stratification, and topography, a closed streamlined anticyclonic vortex, or Taylor column, is expected to remain trapped above the seamount [Hogg, 1973; Huppert, 1975]. Such trapping may enhance nutrients shallower in the water column and if the residence time of a water mass above the seamount is sufficiently long, result in enhanced primary productivity and transfer into higher trophic levels. In this section we consider evidence for such enhancement and the role it plays in different trophic levels.

Nutrients and Primary Productivity

The uplifting of isotherms over seamounts is distinct and occurs with sufficient frequency to provide support for Taylor column dynamics. As an example, isotherms over Minami-Kasuga Seamount in the Mariana Archipelago [Genin and Boehlert, 1985] showed a clear uplift (Fig. 1) which did not reach the surface. Such upwelling at seamounts, like coastal upwelling, will transport nutrients into

the euphotic zone where the primary production is nutrient-limited; an analogous situation exists around islands in stratified seas, where increased tidal mixing may stimulate primary productivity [Simpson et al., 1982]. Observations on a variety of seamounts support this contention; Bezrukov and Natarov [1976] suggested that vertical velocities on the order of 0.00003 to 0.0008 cm·sec^{-1} exist over various seamounts and that differences in the magnitude of upwelling may explain variability in seamount productivity. Vortices associated with seamounts can produce physical structures much like open-ocean cold core rings, except they remain centered over the seamount. Kozlov et al. [1982] describe a "columnar distribution" of temperature, salinity, silicate, and phosphate over one of the summits of Milwaukee Seamount in the southern Emperor Chain, in which elevated nutrient levels corresponding to the values at the seamount flanks reach high into the water column. Two visits, one month apart, to Pulkovskaya Seamount in the South Pacific suggested that vortices existed around the twin peaks and "satellite" vortices remained in surrounding waters. Again, signals were apparent in salinity, temperature, and silicate; silicate concentration at the summit depth of 500 m extended to the surface, with values nearly double that in surrounding waters [Kozlov et al., 1982]. Darnitsky et al. [1984] studied nutrients over Wanganella Bank near New Zealand during six visits from 1974 to 1977. Although upwelling and the resultant nutrient enrichment were clearly observed twice, the water was stratified with no apparent seamount effect during four other transects.

A shorter time scale was addressed in a study by Genin and Boehlert [1985], who conducted a series of transects to describe temperature and chlorophyll distribution over Minami-Kasuga Seamount. On the first of three surveys made within a month, uplifted isotherms formed a subsurface cold dome above the seamount (Fig. 1). The vertical displacement of the uplifted isotherms gradually decreased with distance above the seamount, from a 50 m uplift of the 17° isotherm close to the substratum, to a decay of the cold anomaly at about 80 m depth (180 m above the seamount top). Different deflection trends of isotherms in the vicinity of the substratum around the seamount slope formed a "boundary zone" comprising three distinctive layers composed of downward deflected isotherms from approximately 500 m to about 420 m, a relatively well mixed "transition zone" (Fig. 1) between the 14.5° and 15° isotherms (approximately 50 m above the previous layer), and an upwelling layer shallower than 340 m. These layers may be related to energy dissipation in the benthic boundary layer and agree with the statement by Bezrukov and Natarov [1976] that there is typically a change in the sign of vertical velocity between 300 and 600 m on the flanks of seamounts. On this first survey, calculations based upon seamount morphology suggested that conditions favoring maintenance of a Taylor column were present.

Three chlorophyll profiles taken within the cold dome showed a distinctive maximum between 80 and 100 m depth, whereas the chlorophyll maximum layer at the four control stations was comparatively diffuse (Fig. 2). The causal relationships between the localized upwelling and the biological response are corroborated by the confinement of the chlorophyll increase to depths below 80 m, the uppermost edge of the cold dome. The chlorophyll concentrations at shallower depths above the seamount and at the control stations varied little throughout the area. These results clearly contrast with data from the second and third surveys in which neither cold dome nor chlorophyll increases were detectable along the same transects. These observations suggest that varying strength of oncoming currents result in a varying time scale for presence of the uplifted isotherms. Estimates of the time necessary for the formation of the observed chlorophyll maximum from the first survey, however, suggest a minimum residence time of the hypothesized Taylor column on the order of days [Genin and Boehlert, 1985].

The vertical extent and residence time of seamount-induced upwelling will determine the magnitude of its effect on local biological processes in overlying waters. Unfortunately, the temporal sampling scale of the studies described above is inadequate to determine the temporal dynamics clearly, and knowledge of regional currents is frequently lacking; moreover, the time scales will vary from seamount to seamount, which will have an effect on the manner in which any enhanced primary productivity may reach higher trophic levels. In oligotrophic oceans, phytoplankton production would increase if the uplifted isotherms penetrated into the euphotic zone, replenishing its depleted water with nutrients, as noted by Kozlov et al. [1982] and in the first survey by Genin and Boehlert [1985]. Entrapment on the order of days would probably affect only the primary producers, and hence, a patch of relatively high chlorophyll concentrations would be associated with the seamount. A longer residence time, on the order of several weeks, may locally affect the growth and abundance of zooplankton species; months would be necessary for micronekton [Pudyakov and Tseitlin, 1986]. Lagrangian current observations made above the Emperor Seamounts [Cheney et al., 1980] and the Corner Rise Seamounts [Richardson, 1980] suggested entrapment periods up to several weeks within seamount-generated anticyclonic eddies. Much longer periods (on the order of several months) were inferred from hydrographic and Eulerian current measurements above a deep seamount in the North Atlantic [Owens and Hogg, 1980]. If local enrichment persists for long periods and is a recurrent phenomenon, nektonic organisms may be attracted to or aggregated in these habitats [Uda and Ishino, 1958; Boehlert and Seki, 1984; Uchida and Tagami, 1984]. An analogy may be drawn to demersal plankton in nearshore reef systems [Hobson and Chess, 1978; Alldredge and King, 1985].
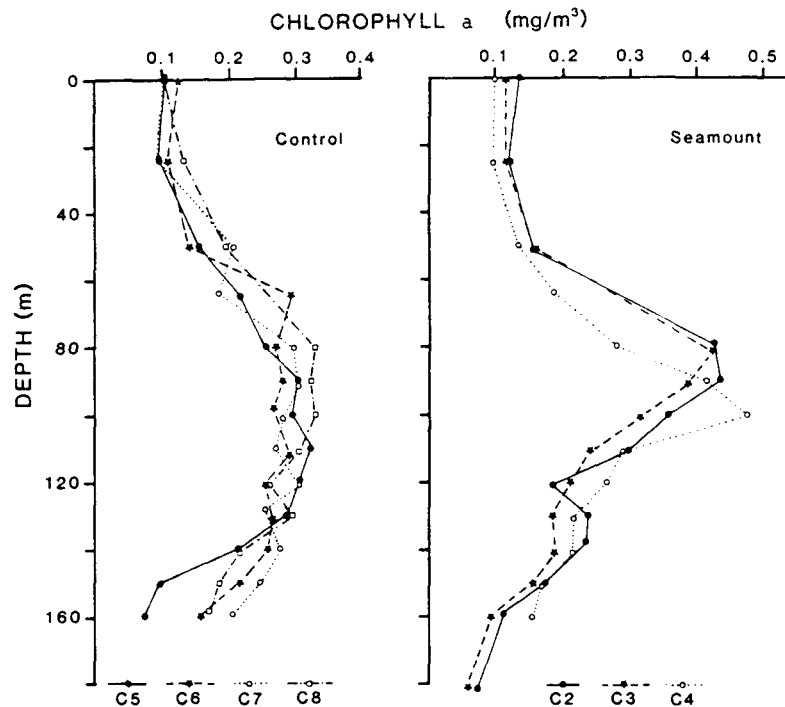
13 March 1984

Fig. 2.   Chlorophyll a profiles above Minami-Kasuga Seamount taken concurrently with the temperature transects shown in Figure 1.   Three stations were occupied over the top of the seamount (right) and at control stations which were 10 km from the seamount summit (left).   (From Genin and Boehlert 1985.)

Zooplankton and Nekton

Evidence concerning densities of planktonic organisms above seamounts is often conflicting. Sorokin and Sorokina [1985] noted no differences between waters above seamounts and surrounding waters with respect to bacterioplankton.   Many surveys in the regions of seamounts, however, indicate two- to eightfold increases in zooplankton abundance in waters over seamounts [Fedosova 1974]; Zaika and Kovalev [1984] summarize results from a variety of Soviet papers.   Zooplankton samples were taken by Genin and Boehlert [1985] in two of their three surveys, one during elevated and the other under normal chlorophyll levels. Zooplankton displacement volume was greater above the seamount only on the first survey; in contrast to the chlorophyll signal, however, zooplankton volumes were higher within the cold dome and above it, possibly indicative of the more vertically mobile nature of zooplankton [Genin and Boehlert 1985].   Whereas the studies referred to above have typically considered zooplankton biomass, it may be more appropriate to consider specific taxa, which may be either more abundant or relatively depleted in waters above seamounts [Hirota and Boehlert, 1985].

A specific component of the plankton studied above seamounts has been the ichthyoplankton.   In the North Pacific, Borets and Sokolovsky [1978] observed no differences in ichthyoplankton abundance or species composition above seamounts as compared to distant waters; Belyanina [1985] had similar results in the Indian Ocean.   Nellen [1973], however, in a study on the Great Meteor Seamount, noted increased abundance of neritic species and depletion of others, most typically midwater fish larvae, above the seamount.   Boehlert [1985] described ichthyoplankton densities from winter and summer cruises at Southeast Hancock Seamount.   Fish larvae at this open-ocean seamount are dominated by midwater rather than neritic species.   In the summer, daytime samples showed no difference between the seamount and reference stations with the exception of the 50-100 m stratum (Fig. 3A).   At night, however, the densities at the reference station were significantly increased as compared to daytime values, but not in the samples taken over the seamount. Samples taken on a winter cruise showed a different pattern from that in the summer (Fig. 3B); ichthyoplankton densities over the seamount were much greater than at the reference station, and the pattern held for night and day.   These data
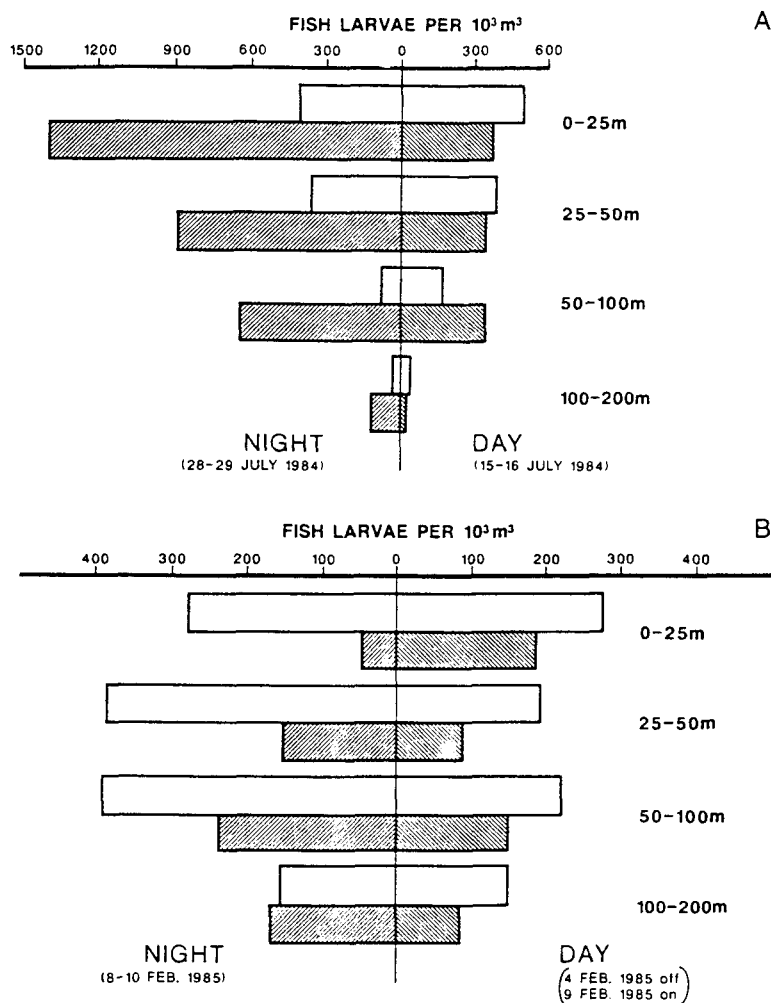
FISH LARVAE PER 10³ m³   A

1500   1200   900   600   300   0   300   600

0-25m

25-50m

50-100m

100-200m

NIGHT   DAY
(28-29 JULY 1984)   (15-16 JULY 1984)

FISH LARVAE PER 10³ m³   B

400   300   200   100   0   100   200   300   400

0-25m

25-50m

50-100m

100-200m

NIGHT   DAY
(8-10 FEB. 1985)   (4 FEB. 1985 off
                     9 FEB. 1985 on)

Fig. 3. Comparison of ichthyoplankton densities above Southeast Hancock Seamount (lat. 29°8'N, long. 178°5'E) with those at reference stations 20 km away. Samples were taken at discrete depths with an opening-closing Tucker trawl. 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. (Presented in Boehlert, 1985.)

suggest that some phenomena differing between winter and summer (or an aliased time scale) impact the abundance of these taxa.

As compared to the passive planktonic species, micronekton and nekton have more control over their movements. Fewer studies over seamounts have been conducted on these species, but Uda and Ishino [1958] suggested that aggregations of such animals may result in enhancement of fishing grounds. Densities may be estimated using hydroacoustic observations and net sampling. Some organisms normally rare in open-ocean areas may be abundant on seamounts. The sternoptychid fish,

Maurolicus muelleri, typically associated with continental shelf-slope breaks, has been observed in abundance over South Atlantic and North Pacific seamounts [Linkowski, 1983; Boehlert and Seki, 1984]. Kozlov et al. [1982] noted vertical columns of scattering layers over two seamounts in the North Pacific but mistakenly considered them to be simply vertical manifestations of the oceanic scattering layers arrayed vertically like the "columnar" distributions of temperature and nutrients. Hydroacoustic observations at night above Southeast Hancock Seamount [Boehlert and Seki, 1984] showed pronounced scattering (Fig. 4).
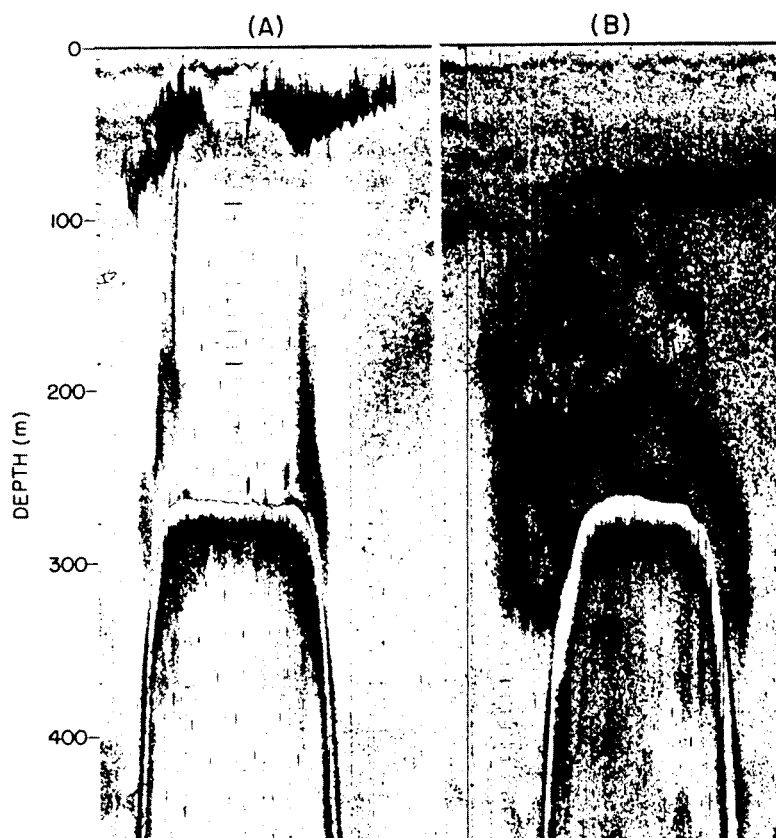
Fig. 4. Acoustic transects over Southeast Hancock Seamount on 17-18 July 1984 taken with a 38 kHz echo sounder. Each transect, from west to east (left to right) near the central axis of the seamount, took approximately 25 min. The distance across the flat portion of the seamount is approximately 1.8 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 1907. B. 0330 h. The layer has developed over the seamount extending from the flanks upwards to near 100 m; it developed this configuration at approximately 2130 and remained in a similar configuration throughout the night, until dispersing in early morning. These scattering targets may have been larger fishes or squids not sampled by our midwater trawl. (Presented in Boehlert and Seki, 1984.)

Scatterers typically remained on the flanks of the seamount by day, but began streaming vertically upward to depths near 50 m early in the evening (Fig. 4A), 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). By contrast, no deep scattering layers in surrounding 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. Subsequent hauls with midwater trawls demonstrated differences in abundance and species composition between waters above the seamount and at the reference stations. Maurolicus muelleri and the lophogastrid mysid, Gnathophausia longispina, dominated the catch over the seamounts. A third species, the sepiolid squid, Iridoteuthis iris, was characteristic of the deeper portions of the seamount scattering layer (Fig. 5A). In waters away from the seamount, oceanic taxa were generally more abundant and the three seamount taxa were either

DENSITY (Ind./10³M³)   A

Maurolicus muelleri

Vinciguerria spp.

Myctophidae

Other Fishes

Iridoteuthis iris

DENSITY (Ind./10³M³)   B

Gnathophausia longispina
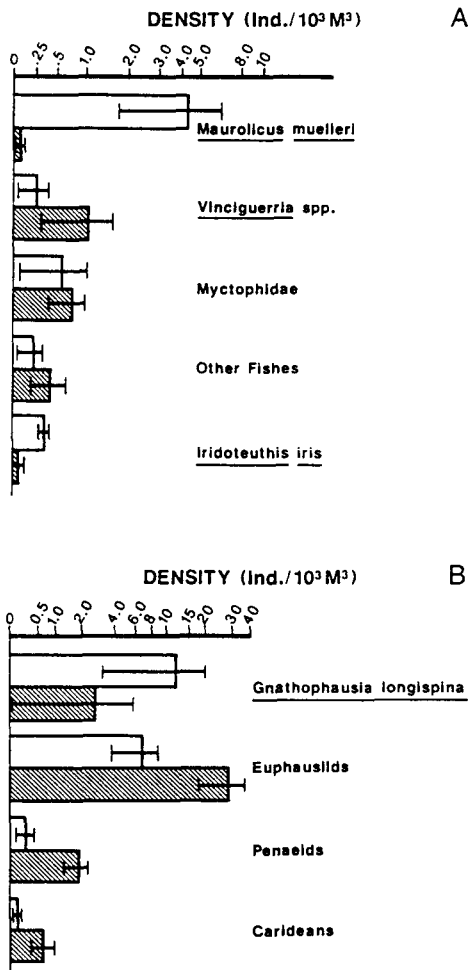
Euphausiids

Penaeids

Carideans

Fig. 5. Comparison of densities of selected micronekton taxa captured above Hancock Seamount with those taken at reference stations 5 to 20 km away in summer, 1984. Twelve samples were taken above the seamount and six at reference stations with a 6-ft Isaacs-Kidd midwater trawl. A. Fishes and squid. B. Crustacea. 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; note that abundances are on a log scale. (Presented in Boehlert and Seki 1984.)

absent or in low abundance (Fig. 5B). It would appear that this seamount, and others described above, have important effects upon the pelagic ecosystem. A better understanding of the local physical and biological oceanography will be necessary to determine the nature and cause of these effects.

Ecology of Seamount Benthos

Evidence that seamounts are inhabited by unique, and sometimes rich, benthic communities was first obtained in the surveys of Vema Seamount (South Atlantic) and Bowie and Cobb Seamounts (northeast Pacific), all shallow seamounts where scuba diving was used [Simpson and Heydorn, 1965; Scagel, 1970; Birkeland, 1971]. Developments in deep-sea photography allowed the first visual examination of deeper seamounts. Some of the first photographs [Heezen and Hollister, 1971] showed current-swept beds inhabited by corals, sea pens, anemones, sponges, crinoids, and other sessile suspension feeders on Eltanin Seamount (southeast Pacific, 162 m), Kelvin Seamounts (western North Atlantic, 1,419 m, 903 m), and Ampere Seamount (North Atlantic, 143 m, 529 m). Other studies have revealed dense populations of the gorgonian coral, Ellisella flagellum, seen in photographs taken on Josephine and Great Meteor Seamounts (east Atlantic, 200-300 m; Grasshoff, 1972] and the high abundance of sponges, hydroids, bryozoans, and serpulid tubeworms on the top of Patton Seamount (Gulf of Alaska, 433 m; Raymore, 1982].

Most of the photographic investigations noted above were rather limited in spatial coverage, with photographs taken at only a few locations on each seamount. Only with the use of more advanced photographic instruments could the distributional patterns of deep seamount benthos be studied. Genin et al. [1986] used the Deep Tow [Spiess and Tyce, 1973] and Grigg et al. [1987] used towed sleds to take hundreds of photographs along several transects on different parts of seamounts. Manned submersibles have also been used recently in seamount studies, allowing detailed surveys of megafauna as well as small meiofauna [Levin et al., 1986; Lissner and Dorsey, 1986]. Submersible investigations, which allow detailed observations and even experimental manipulations, hold great promise for understanding seamount benthos.

Seamounts are highly diverse habitats. A single seamount usually extends over a large depth interval, sometimes from the euphotic zone to the abyss. Substrata of seamounts vary from exposed rocky bottom to a continuous thick layer of sediments. The latter is usually found on the top of deep guyots and in topographic depressions, whereas rocky outcrops and extensive hard-bottom areas characterize the steep flanks as well as the tops of shallow guyots [Karig et al., 1970; Lonsdale et al., 1972; Raymore, 1982; Genin et al. 1986]. Sediments on seamounts can vary in grain size and can be rippled at one site and smooth at another. The sediment distribution pattern can be greatly affected by the topographically-induced current regime, creating sometimes a moat around the seamount base [Roberts et al., 1974]. Types of hard bottom on seamounts are highly variable, ranging from carbonate rocks and pillow basalt to rocks encrusted with a hard ferromanganese layer. Remarkably different substrata can even be found

on a single seamount. In spite of this great
variability, some unique environmental conditions
seem to lead to common biological characteristics
of seamount benthos. These features include the
clarity of overlying waters and extended light
penetration, the presence of deep rocky substra-
tum, and the exposure to strong currents. The
effects of these conditions on the structure of
biological communities on seamounts are the focus
of this section.

Shallow Seamounts--Effects of Water Clarity and Isolation

Far away from sources of terrigenous turbidity,
mid-ocean seamounts (like many oceanic islands)
are characterized by exceptionally clear overlying
waters, where the attenuation of light is far
lower than in coastal waters. Consequently,
benthic autotrophs may occur in greater depths.
The deepest known plant life, for example, has
recently been discovered on San Salvador Seamount
in the Bahamas, where an undescribed species of
coralline alga was found at 268 m [Littler et al.
1986]. The flat top of this seamount contains a
rich and exceptionally diverse multi-layer commun-
ity of macroalgae with planar algal cover (under-
story and canopies) exceeding 100%. On Tanner and
Cortes Banks (off southern California), a dominant
macroalga, Eisenia arborea, grows as deep as 40 m,
whereas its lower limit at coastal sites in the
Southern California Bight is between 5 and 12 m
depth [Lewbel et al., 1981; Lissner and Dorsey,
1986]. Macroalgal species on these and other
banks exhibit similar depth extensions [Scagel,
1970; Lissner and Dorsey, 1986]. Most of these
species are usually found in the lower intertidal
or upper subtidal zones. This extension was also
the case with some intertidal animals, such as the
mussel, Mytilus californianus, found in relatively
greater depths on Bowie Seamount [Scagel, 1970]
and on a submerged pinnacle off the northwest
coast of Washington [Paine, 1976]. Depth exten-
sions of animals were attributed to biological
factors, such as the rarity or absence of preda-
tors [Paine, 1976]. The asteroid, Pisaster
ochraceus, determines the lower limit of Mytilus
in coastal regions but is rare on the submerged
pinnacle due to the lack of an intertidal zone.
Small recruits of Pisaster are found primarily in
the lower intertidal zone where they feed on small
barnacles [Paine, 1976].

In addition to extensions of depth ranges,
distinctive differences between animal communities
on seamounts and those at adjacent coastal sites
at corresponding depths have been described on
several shallow seamounts [Birkeland, 1971; Lewbel
et al., 1981]. Suspension feeders are typically
in much greater abundance on Tanner and Cortes
Banks than in corresponding coastal regions
[Lewbel et al., 1981]. The scallop, Hinnites
multirugosus, dominates the entire primary sub-
stratum on vertical surfaces of Cobb Seamount,
whereas it exhibits a scattered distribution in

coastal areas of the northeast Pacific [Birkeland
1971]. Tunicates, which frequently dominate rocky
areas on the coasts of Washington, are represented
by a single species on Cobb Seamount, and neither
hydroids nor barnacles have been observed on the
seamount. On the other hand, the community on
Cobb Seamount differs from that on Bowie Seamount;
barnacles and hydroids are found on the latter but
not on the former, and different molluscs are
dominant at each site. Such changes are probably
caused by inter-site differences of ecological
conditions combined with differences of coloniza-
tion history. The presence of brooding species
(the asteroid Leptasterias) and species with no
planktonic larvae (the gastropod Searlesia dira)
on Cobb Seamount [Birkeland, 1971] suggests that
rare colonization events can affect the structure
of the community on each seamount. Propagules of
the brooding asteroids, for example, probably
reached Cobb Seamount with drifting kelp [Birke-
land, 1971].

Deep Seamounts--Effects of Substratum and Currents

The most distinctive characteristic of deep
seamounts is the occurrence of extensive areas of
hard substratum. Unfortunately, most information
on the abundance of deep hard-bottom species on
seamounts is incomplete, largely due to the small
number of detailed surveys conducted. Further-
more, most of the observations were obtained with
dredges or photography, so that very little is
known about the abundance of smaller organisms.
Large suspension feeders, including sponges, horny
corals (gorgonians), black corals (antipath-
arians), ahermatypic scleractinian corals,
anemones, tunicates, brisingid seastars, and
crinoids, are the dominant taxa which have been
observed. Their abundance generally decreases
with depth [Grigg et al., 1987]. Photographs
taken shallower than 1,000 m usually exhibit
several taxa in each frame, sometimes forming
dense communities (Fig. 6, and Heezen and Hollis-
ter, 1971; Grasshoff, 1972; Raymore, 1982; Genin
et al., 1986]. Rich gorgonian fields occur on
several seamounts (depth <1,000 m) in the Emperor
Seamount chain (northwest Pacific). The discovery
of these fields in the late 1970's caused a sharp
decline in prices of precious corals on the world
market [Grigg, 1984].

In oligotrophic oceans, even shallow seamounts,
such as Cross Seamount near Hawaii (summit depth
300 m), exhibit sparse communities [Grigg et al.
1987], whereas relatively high densities of large
suspension feeders are sometimes found in greater
depths on seamounts located in fertile waters
(e.g., on Kelvin Seamount at 1419 m depth; Heezen
and Hollister, 1971]. In addition to the fer-
tility of overlying waters, differences in the
abundance of organisms on different seamounts can
be related to local environmental conditions and
to availability of sources of larvae (i.e., the
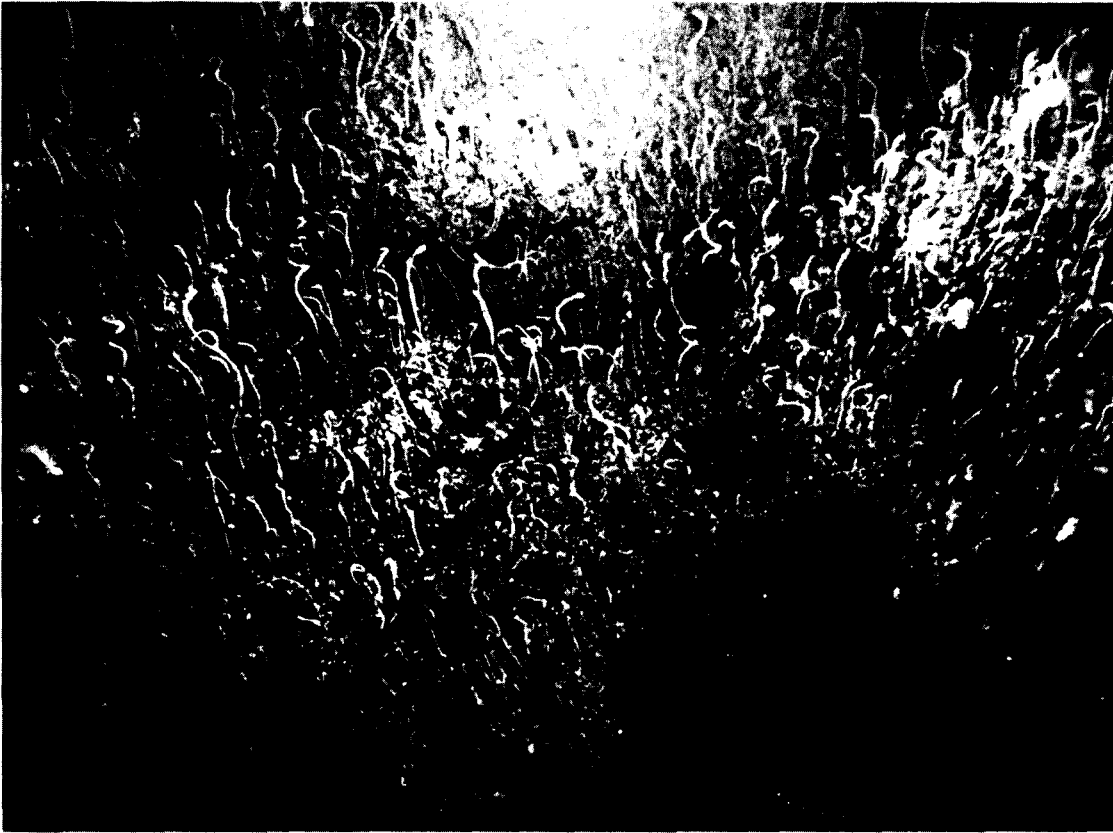presence of adult populations upstream of a sea-

Fig. 6. Antipatharians, sponges, and other suspension feeders near a satellite peak at
700 m depth on Jasper Seamount in the northeast Pacific. Stichopathes sp., the whip-
like black coral, is the most abundant megafaunal species between 600 and 1,000-m
depth.

mount; Lutjeharms and Heydorn, 1981b; Grigg et
al., 1987].

The presence of several satellite peaks on
Jasper Seamount allowed Genin et al. [1986] to
separate the effects of depth and topography on
the abundance of animals. It was expected that
passive suspension feeders would be generally more
abundant at shallower depths, where the concentra-
tion of particulate food in the impinging waters
is greater. The observations, however, showed
that within a certain depth range the distance
from a peak is a key factor in determining animal
densities. The densities of a dominant species on
Jasper Seamount, the black coral, Stichopathes
sp., were significantly higher near peaks than in
mid-slope areas at corresponding depths (Fig. 7).
A similar increase in the densities of corals on
the upper part of a slope, near a peak, has been
observed at ca. 2,000 m depth on Horizon Guyot

(central North Pacific, A. Genin and K. L. Smith,
Jr., unpubl. manuscr., 1986). Other distribu-
tional patterns of large suspension feeders on
seamounts further support the hypothesis that the
abundance of animals on seamounts is determined by
factors related to the local topography. These
patterns can be separated into three spatial
scales, namely patterns observed on the entire
area of a seamount, patterns on topographic
features such as knobs and pinnacles, and small-
scale patterns such as those seen within a photo-
graph. The large-scale patterns include the
above-mentioned increased densities near peaks.
They can be divided into patterns on narrow taper-
ing peaks and those on wide or flat peaks. Densi-
ties on narrow peaks are greatest near the crest,
whereas densities on flat tops of guyots and on
gently sloping peaks are higher near the rim than
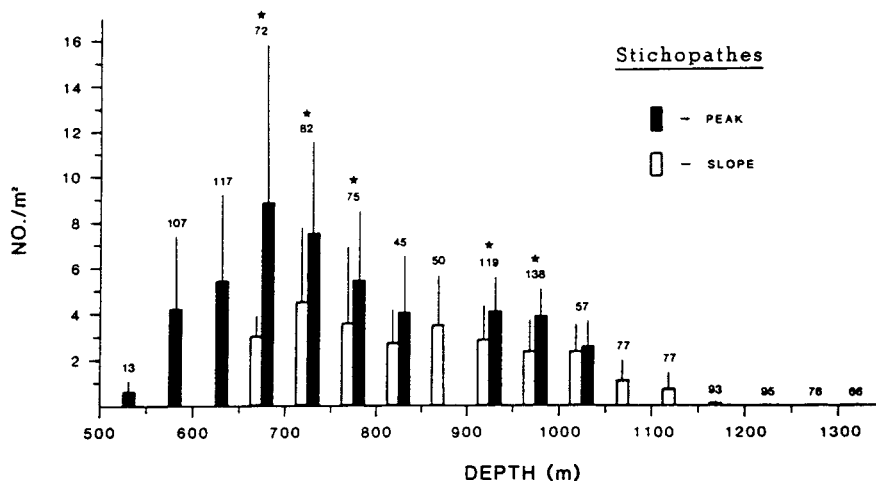near the center (Fig. 8 and Genin et al., 1986,

Fig. 7. Densities of Stichopathes (mean ± s.d.) at different depth intervals on Jasper Seamount. The photographs were divided into those near peaks (solid bars) and those >150 m below a peak (open bars). Stars indicate the intervals in which the mean near-peak density is significantly higher than the mean mid-slope density (P < 0.001, Mann-Whitney U test). The number of photographs taken at each depth interval is indicated above the corresponding bar. (From Genin et al., 1986.)

Jasper Seamount; Grigg et al., 1987, Cross Seamount). A similar increase of coral densities was observed along the rim of Fieberling Guyot (eastern North Pacific, ca. 500 m depth; A. Genin, unpubl. data). On the scales of tens of meters, animal densities are usually greater on topographic prominences, such as pinnacles and knobs, than in surrounding areas (e.g., Fig. 8). On the smaller scale, suspension feeders are frequently aggregated on upper parts of rocks, and small animals were found on protruding parts of larger organisms, such as sponges.

The occurrence of similar distributional patterns on different seamounts, combined with hydrodynamic theories and observations, suggests that a topographically induced current regime is a key factor in determining the abundance of suspension feeders on deep hard-bottom seamounts. Two different mechanisms may enhance currents near the edges of wide peaks. First, the flow of waters impinging on the flank may be upwelled above a seamount's top. Due to conservation of potential vorticity, an anticyclonic motion is induced, resulting in an accelerated flow on the left side of a seamount (looking downstream) and deceleration near the center and on the right [Huppert, 1975; Huppert and Bryan, 1976]. Alternating tidal flows would thereby cause intermittent acceleration periods near the edges and recurrent deceleration near the center of wide peaks and guyots. The other mechanism is related to the reflection of internal waves along a sloping bottom, where intensification of the flow occurs, especially for those waves with frequencies within an octave of a critical frequency defined by the bottom slope.

stratification, and Coriolis parameter [Wunsch 1969; Eriksen, 1982, 1985]. Such an intensification is not expected to be distinctive on the flat or gently sloping areas at the center of guyots and wide peaks, where animal densities are low.

Existing physical theories do not predict the occurrence of stronger currents near a crest of a peak as compared with a mid-slope site at the same depth and on a similar slope angle. Hydrographic observations, however, suggest that the upwelling above such peaks is confined to the proximity of the crest and does not occur over mid-slope areas [Bezrukov and Natarov, 1976; Fukasawa and Nagata 1978; Genin and Boehlert, 1985; Roden and Taft 1985]. Short-term current measurements made by Genin et al. [1986] on Jasper Seamount also showed differences between a peak and a mid-slope site: the average current speed near a peak was about twice the mean speed recorded at a mid-slope site at the same depth. The mid- and small-scale increases of densities of suspension feeders on knobs, pinnacles, and on the top of protruding rocks can be similarly explained by an exposure to enhanced currents as these structures protrude to higher elevations above the bottom and are therefore exposed to more energetic zones of the benthic boundary layer [Butman, 1986; Grant and Madsen, 1986]. Even on such small-scale features, however, variability in colonization rates may be related to small-scale flow structure [Nowell and Jumars, 1984]. Genin et al. [1986] proposed two different mechanisms through which intensified currents can induce higher animal densities. In the "settlement pathway," a site is colonized by relatively more recruits simply because more
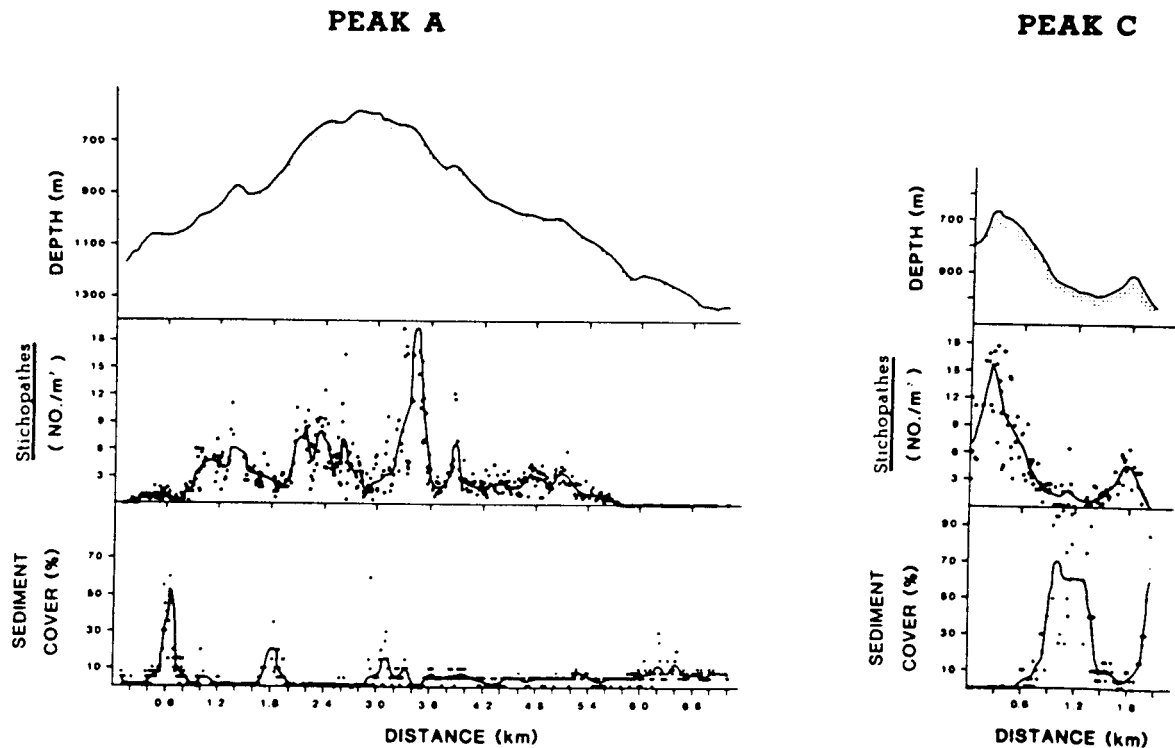
PEAK A   **PEAK C**

Fig. 8. Bathymetry, densities of Stichopathes, and sediment cover across two satellite peaks on Jasper Seamount. Each dot indicates the animal density or sediment cover in a single photograph. Solid lines indicate 9-point running means. Note that the animal densities follow the bathymetric line on the sharp peak (C) whereas lower densities are found near the center of the wide peak (A) than near its edges. Animal densities are relatively higher on small topographic prominences such as those at 1.4 and 3.9 km along the transect. Note the sharp increase of sediment cover in the topographic depression near peak C. (From Genin et al., 1986.)

water, and thereby more larvae, flow through per unit of time; in the "feeding pathway," more water flows past suspension feeders at sites characterized by stronger currents, resulting in increased feeding and growth rates and possibly higher survival rates of small recruits. The actual mechanisms involved are yet to be experimentally tested.

Very little is known about soft-bottom fauna on deep seamounts. Unlike hard-bottom epifauna, infauna in sedimentary substrata cannot be observed by photography. In a recent study of deep (1,000 to 3,000 m) seamounts in the Pacific Ocean off Mexico, Levin et al. [1986] used a submersible to investigate the effects of giant protozoans (xenophyophores) on local soft-bottom communities. Xenophyophores are abundant on seamounts where they agglutinate sediments to form large tests (up to 25 cm diameter) which protrude above the sediment. Sediments immediately surrounding these organisms exhibit higher densities and diversities of metazoan species relative to

control sediments collected at distances of 1 m from those protozoans. Levin et al. [1986] propose that xenophyophores contribute to maintenance of high benthic diversity by altering hydrodynamic conditions and by providing metazoans with substratum, food, and refuge. The diversity of soft-bottom habitats on seamounts has not been compared with the surrounding deep sea; this would make an interesting investigation from a submersible, since a wide depth range occurs at a single site on soft-bottom seamounts.

The Role of Seamounts in
Fisheries Productivity

Seamounts and banks may aggregate resident demersal and transient, pelagic organisms which can support fisheries [Uda and Ishino, 1958; Uchida et al., 1986]. Polovina [1985] compared seamounts with bank and island systems and found higher densities of the same species on the seamounts. A variety of demersal resources in high
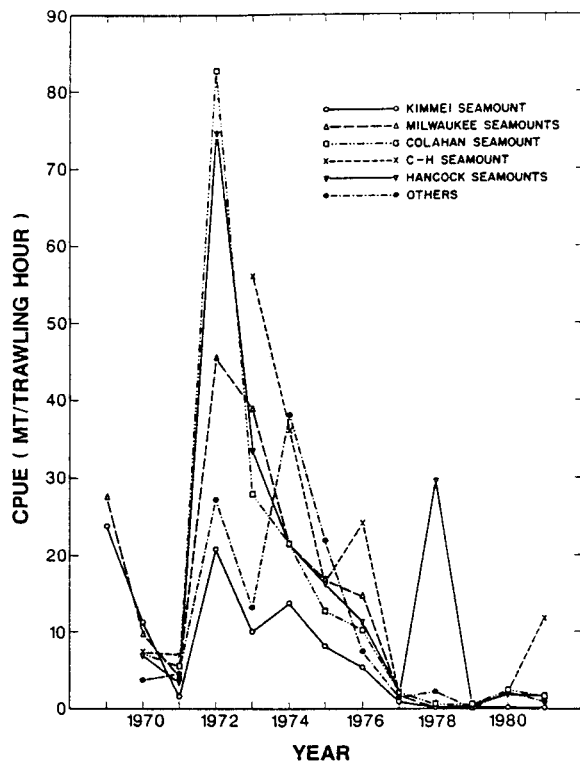
Fig. 9.   Annual data on catch-per-unit-effort (an
index of abundance) of Japanese trawlers for
pelagic armorhead on several of the southern
Emperor-northern Hawaiian Ridge seamounts, 1969-
81. These data show the sharp decline in stock
abundance. The Japanese catch was about one-fifth
that of the Soviets; combined, they took
approximately one million metric tons of this
species off these seamounts during this period.
(From Wetherall and Yong, 1986.)

abundance has been noted on seamounts including
fishes [Sasaki, 1986], lobsters [Lutjeharms and
Heydorn, 1981a], crabs [Hughes, 1981; Alton, 1986]
and precious corals [Grigg, 1986; Genin et al.
1986]. Pelagic species such as tunas and squid
may seasonally feed in waters above seamounts
[Inoue, 1983; Yasui, 1986], as do some marine
mammals [Hui, 1985]. In the open ocean, seamounts
thus function as sites of increased production or
aggregation of higher trophic level organisms.
   A specific example of high fisheries produc-
tivity is provided in the southern Emperor and
northern Hawaiian Ridge seamounts. Between 1967
and 1975, nearly one million metric tons of
pelagic armorhead, Pseudopentaceros wheeleri, were
taken by Soviet and Japanese trawlers, and stand-
ing stocks were estimated at nearly 400,000 metric
tons [Borets, 1975; Sasaki, 1986]. Japanese data
on catch per unit effort (Fig. 9) demonstrate

extremely high catch rates which declined drasti-
cally in later years of the fishery. Some of the
same physical mechanisms which alter the patterns
of distribution and abundance of the taxa as
described earlier for Hancock Seamount may be
invoked to explain the availability of the energy
necessary to maintain high densities of fish here
and at other seamounts. First, convergent flow
resulting in accumulation and greater flux of
oceanic plankton and micronekton may provide prey
[Isaacs and Schwartzlose, 1965; Darnitsky et al.
1984; Tseitlin, 1985]. Secondly, as described
earlier, locally enhanced productivity may be
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. Energy for the high biomass
demersal fish resources, however, appears to be
derived from oceanic rather than seamount-derived
sources. This assertion is supported by diet
studies of pelagic armorhead [Fedosova, 1976],
species on seamounts in the Indian Ocean [Parin
and Prutko, 1985], and elsewhere [Kashkin, 1984].
Simulation models of seamount fish populations
[Tseitlin, 1985; Pudyakov and Tseitlin, 1986]
suggest that such allochthonous energy inputs are
necessary for population maintenance.
   An intriguing question about these animal
resources, given that most have pelagic larvae, is
the mechanism of recruitment back to the seamount.
One of the first suggestions of such a mechanism
invoked the concept of stationary Taylor columns
over seamounts for maintenance of pelagic larvae
[Shomura and Barkley 1980]. This hypothesis is an
extension of the ideas on the conservation of
insular plankton described by Boden [1952]. Main-
tenance of pelagic larvae in closed circulations
above large bank systems has recently been demon-
strated in several locations [Dooley 1984; Sundby,
1984; Smith and Morse, 1985]. Others have sug-
gested that seamount populations are derived from
upstream source populations; the distances pro-
posed have been as great as 1,100 nmi [Lutjeharms
and Heydorn, 1981b]. In either of these cases,
however, physical variability can lead to inter-
annual variability in recruitment strength; such
fluctuations may be characteristic of seamount
resources [Lutjeharms and Heydorn 1981a; Wetherall
and Yong, 1986]. Given the small geographic
extent of seamounts and the variability in
recruitment, great care must be taken to manage
seamount resources and prevent overexploitation
[Boehlert, 1986; Sasaki, 1986].

Conclusions and Suggestions for Future Research

   As we have described in this paper, seamounts
are sites where physical perturbations result in
development of unique ecosystems. Understanding
variability in the biological productivity of
seamounts is a challenging research problem which
will require interdisciplinary research. Meso-
scale physical oceanographic studies will be
necessary to define the conditions for development

of eddies, Taylor columns, and other features of
flow complexity. Small-scale studies of upwell-
ing, turbulent mixing, and benthic boundary layer
effects will better characterize the local condi-
tions near the seamount. Concurrent studies of
biological oceanography of the water column over
seamounts can define the variability of nutrients
and primary productivity and their residence
times. By understanding the seasonal and inter-
annual variability of these phenomena, we should
be able to better define the importance of
enhanced productivity to higher trophic levels and
to determine the role of currents in concentrating
or increasing the flux of allochthonous energy
sources. In addition to these temporal components
of variability, comparative studies of seamounts
can provide an understanding of spatial varia-
bility. Given information on bottom topography
and ocean currents, perhaps we can develop gener-
alities or predictive capabilities concerning
seamount productivity. In this comparative vein,
we should consider other topographic features,
including banks, coastal headlands, and islands,
where related phenomena may occur.

Benthic communities on seamounts may provide an
initial indication of productivity, since the
benthos may serve as an integrator of productivity
of the overlying water column; sediments, where
they occur on or around seamounts, may provide a
historical record of the patterns of such produc-
tivity. Most studies of seamount benthos, how-
ever, have been observational or descriptive. A
greater understanding of factors structuring the
communities on deep seamounts will undoubtedly
require the use of submersibles. The remarkable
changes of environmental conditions over rela-
tively small distances on seamounts, combined
with manipulative capabilities of research sub-
mersibles, could prove most useful in conducting
controlled experiments to define the mechanisms
which structure deep-sea communities.

Finally, the local modification of physical
and biological conditions by mid-ocean seamounts
provides a unique opportunity in marine research.
Experimental manipulations commonly performed in
marine intertidal and subtidal research have
significantly contributed to the understanding of
key ecological processes. Such manipulations
cannot typically be performed on scales large
enough to be applicable to the open ocean. Warm-
and cold-core rings have provided natural experi-
ments in which isolated pelagic populations have
been studied [Backus et al., 1981; Olson and
Backus, 1985]. Seamount-induced upwelling and
eddy generation may provide similar "manipula-
tions." Processes related to the formation and
maintenance of the deep chlorophyll maximum, for
example, may be studied with the temporally
varying upwelling induced by seamounts. In addi-
tion, relationships between different time scales
of physical events and the associated biological
response at different trophic levels can contrib-
ute significantly to our understanding of marine
ecosystems.

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