Productivity and Population Maintenance of Seamount Resources and Future Research Directions

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ABSTRACT

Seamounts represent ocean features whose potential for biological resources has been largely overlooked. The recent discovery of abundant fish resources in the southern Emperor Seamounts region, however, has led to fisheries development and exploitation. We have little understanding of basic biological and population characteristics such as recruitment patterns, age distribution, the stock-recruit relationship, natural mortality, and trophic relationships among seamount species to form the basis for appropriate management. Seamount fisheries differ in many respects from other fisheries so that innovative methods are needed to evaluate resource characteristics. Available information suggests that interaction of seamounts with ocean currents results in flow complexities including Taylor columns and eddies which may either increase productivity or aggregate prey organisms. Thus, seamounts may play important roles in the concentration of biological resources. Understanding the productivity and sustainability of these resources requires multidisciplinary approaches involving physical and biological oceanographic research.

INTRODUCTION

Seamounts are a dominant feature of the geomorphology of the Pacific Ocean, yet they have received relatively little study. Logistic constraints have generally limited biological investigations to small-scale efforts designed to consider the fauna present in particular locations (Pratt 1967; Raymore 1982). In the northern and central Pacific, however, the discovery of exploitable biological resources has intensified the study of the value and sustainability of seamount fishery resources in the Gulf of Alaska (Hughes 1981) and in the southern Emperor-northern Hawaiian Ridge (SE-NHR) region (Humphreys et al. 1984). Seamounts in the Gulf of Alaska have fish populations similar to those in coastal waters but unexpectedly high densities of several species of crabs (Hughes 1981), but no directed fishery has developed to exploit these resources. In the SE-NHR seamount group (Fig. 1) the development of a fishery preceded fisheries research. Since that time, new fisheries have developed, including those for bottom fishes besides pelagic armorhead, *Pseudopentaceros wheeleri* (Humphreys et al. 1984), precious corals (Grigg 1982), albacore (Yasui 1986), skipjack tuna (Inoue 1983), and squid.

Traditional fisheries research is difficult to conduct on seamounts. Seamounts are generally remote, making seasonal, repeated sampling difficult. Often, the fine-scale topography of the shallow portions of the seamounts is poorly known, although bathymetric studies continue (Smoot 1985). In the SE-NHR seamounts relatively little is known about the life history and ecology of the dominant species, their habitats, and the associated ecosystem; thus new approaches will be necessary to assess and determine the sustainability of the resource.

Although limited in area, seamounts may serve as locations for concentration and transfer of energy from the pelagic to demersal ecosystems. Demersal resources of seamounts may maintain high biomasses as a result of localized enhancement or concentration of the productivity of overlying waters. Our understanding of this productivity is largely at the hypothetical stage and few data exist. It is thus difficult to draw conclusions about possible mechanisms that maintain these large demersal populations. If productivity is indeed high, one can understand how large populations of fishes, deriving nutrition from overlying waters, could develop over time. A major concern, however, is the sustainability of these populations. On mid-Pacific seamounts, currently depressed populations of pelagic armorhead may not allow us to estimate the maximum sustainable yield. Recruitment rates and variability, the stock-recruitment relationships, and the basic ecological processes associated with seamount populations are unknown. Further, it is difficult to find other populations with which to make valid comparisons. Fish populations of seamounts are geographically isolated, but no evidence exists to suggest that stocks of dominant species are independent between seamounts. These issues will be important to address as we consider further research on seamount resources. It is the purpose of this paper to discuss hypotheses about the maintenance of seamount populations and to suggest future research.

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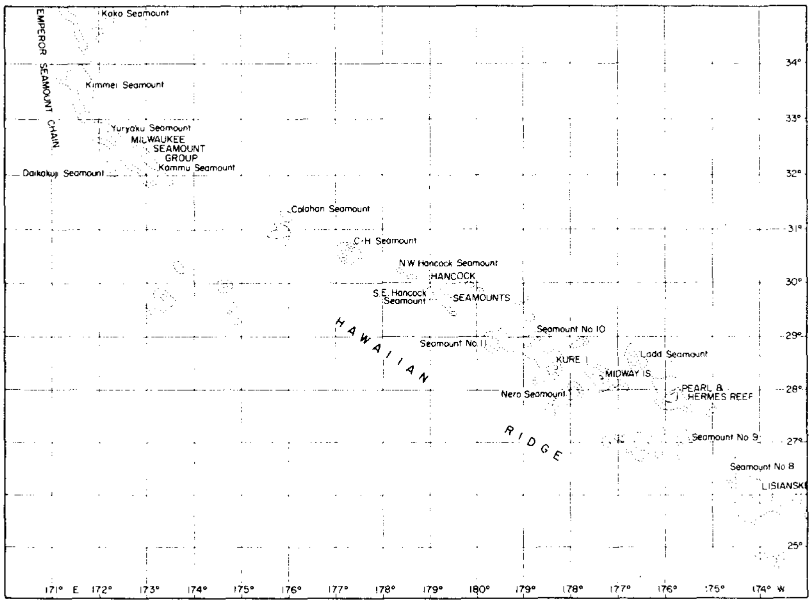

Figure 1.—The southern Emperor-northern Hawaiian Ridge seamounts. The range of the armorhead and alfonsin are largely restricted to the north by the depth of the seamounts and to the south most likely by temperature. Current flow in this region is dominated by easterly flow from the Kuroshio north of the subtropical front, but this front can vary seasonally (and interannually) between lat. 28° and 32°N (Roden 1970); south of the front, westerly flow may be observed.

ENHANCED PRODUCTIVITY OVER SEAMOUNTS

The idea that productivity is enhanced over submarine banks and seamounts is associated with complexities of physical oceanography and is derived, in large part, from the work of Uda and Ishino (1958). They suggested that topographically generated eddies enhance productivity, which is reflected in increased fish catch. In this section I will consider the evidence for increased productivity and the potential for advection and concentration of pelagic productivity from other areas to the seamount regions.

Waters overlying seamounts are often characterized by high standing stocks of plankton (Uda and Ishino 1958; Fedosova 1974; Bezrukov and Natarov 1976). Several ideas exist about the high productivity in the region of seamounts. The effects of seafloor topography on ocean currrents have been reviewed by Hogg (1980). Generally oceanography around seamounts is complicated. Taylor columns, semistationary eddies located above seamounts, have been theoretically predicted for several decades (Taylor 1917; Huppert and Bryan 1976) and actually observed over some seamounts (Owens and Hogg 1980; Richardson 1980). Taylor columns may also be generated over the SE-NHR seamounts, where eddies have been observed (Bezrukov and Natarov 1976; Cheney et al. 1980), but most oceanographic surveys sample too large a grid to detect these open-ocean mesoscale phenomena (Roden 1986). Eddies shed downstream of the seamounts, however, are an important source of variability in the oceanography of the North Pacific (Royer 1978).

Taylor columns may be important in maintaining planktonic populations and may indeed produce increased primary and secondary productivity. 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). The upwelled cold water could bring nutrients to the euphotic zone, resulting in increased productivity. The stationary nature of this eddy over the seamount would also decrease the probability of advection of this productivity from the seamount, making it available to seamount populations. Some support for these arguments is provided by a comparison of waters over seamounts with adjacent waters; differences have been noted in chlorophyll content (Genin and Boehlert 1985), plankton biomass (Bezrukov and Natarov 1976), ichthyoplankton (Nellen 1973; Boehlert 1985), and micronekton (Boehlert and Seki 1984). On a small seamount in the Marianas, however, Genin and Boehlert (1985) showed that the phenomenon seemed to be transitory, but dependent upon the oncoming current strength and the morphology of the seamount.

Uda and Ishino (1958) suggested that increased pelagic productivity may enhance productivity on banks and seamounts, and stated "the concentrated areas of food animals including nekton, plankton and benthic fauna are fertilized by upwelling and accumulated or hydrobiologically limited by convergence." Indeed, the densities of pelagic armorhead alone produced catch rates of some 96 metric tons (MT) per trawling hour on Colahan Seamount in 1972 (Humphreys et al. 1984). Estimated standing stock of this species in the SE-NHR seamount region was as high as 396,000 MT in 1969 (Borets 1975; see Table 1). This species, which forms aggregations off the bottom during daytime and feeds on macroplanktonic and micronektonic animals, is considered to be semidemersal at the seamounts. The biomass of prey organisms necessary to support such a large localized predator population must be immense; it is doubtful that the standing stock under average conditions of the North Pacific Ocean could support this biomass of pelagic armorhead. An analogy may be drawn with surface schooling tunas, which apparently depend upon fronts for prey aggregation (Murphy and Shomura 1972).

Table 1.—Catch and effort from the Japanese and Soviet fisheries for armorhead, *Pseudopentaceros wheeleri*, on the SE-NHR seamounts and estimates of boarfish stock size, 1968-75. Data are from Takahashi and Sasaki (1977) for the Japanese data and Borets (1975) for the Soviet data. Soviet catch data have been converted to weight from numbers by assuming a mean weight of 0.5 kg/fish. Note the difference in units of effort between the Japanese and Soviet data.

Indices	1968	1969	1970	1971	1972	1973	1974	1975
Japanese data								
Catch (10^3 MT)	—	3.28	30.0	5.9	29.9	25.0	34.5	19.0
Fishing effort (trawling hours)	—	157	2,807	1,304	496	740	1,583	1,377
Soviet data								
Catch (10^3 MT)	49.5	162.5	145.0	17.0	98.0	170.5	39.5	46.5
Fishing effort (vessel days)	1,069	3,282	3,516	467	1,883	4,044	1,589	2,047
Stock size (10^3 MT)	310.5	396.0	329.5	221.5	364.0	355.5	173.0	160.5
Recruitment (10^3 MT)	180.5	148	77.5	193.5	140	35	51	—

Mechanisms which aggregate food organisms produced elsewhere may also contribute to energy flow on seamounts. Pereyra et al. (1969), for example, observed concentrations of demersal yellowtail rockfish, *Sebastes flavidus*, feeding in areas where midwater organisms were being advected onto the continental shelf. Isaacs and Schwartzlose (1965) observed a similar pattern on an offshore bank and suggested that such fish populations thus may not be limited by local productivity, but rather depend upon oceanic productivity and advection or hydrographic aggregation of prey sources. Midwater fishes and other organisms in scattering layers may reach very high densities during daytime (Backus et al. 1968). Alldredge and Hamner (1980) described a hydrodynamic aggregation of plankton some fortyfold over mean densities in an eddy system near a coastal headland and suggested that it may have important effects upon fish distributions. Similarly, Olson and Backus (1985) provide data and model a concentrating mechanism for midwater fishes at fronts. Interaction of currents with coastal headlands or undersea banks may be responsible for dense aggregations of several species of fishes, including widow rockfish, *Sebastes entomelas*, in the northeastern Pacific and orange roughy, *Hoplostethus atlanticus*, off New Zealand (Robertson and Grimes 1983).

Similar mechanisms of aggregation probably exist for seamounts. Hamner and Hauri (1981) have described the aggregation mechanism for a small reef, which may be analogous to an isolated seamount. In open ocean areas, where eddies have been studied, the results are equivocal; Hall and Quill (1983) observed increased sound scattering inside as compared to outside an eddy in two out of three instances. Most studies of ocean eddies, however, deal with moving eddies which often differ faunistically from the surrounding water (Griffiths and Brandt 1983) and may thus differ from those in seamount areas. Eddy research is a relatively new field and the effects on the biota are poorly understood (Owen 1981; Angel and Fasham 1983). Pelagic sampling of seamount-generated mesoscale eddies, especially for prey consumed by dominant species, will be important for understanding the mechanisms of enrichment. High abundances of micronekton may exist over seamounts, but these species may be seamount-associated rather than pelagic, such as the sternoptychid fish *Maurolicus muelleri* and the mysid *Gnathophausia longispina* over Hancock Seamount (Boehlert and Seki (1984).

MECHANISMS OF RECRUITMENT OF DEMERSAL POPULATIONS

Understanding recruitment mechanisms and variability will be critical to understanding the sustainability of seamount resources. Given the high density of virgin stocks (Table 1) and their apparent reliance on prey produced elsewhere, it is probable that space is not limiting, at least for pelagic armorhead. For pelagic armorhead, it is probable that recruitment varies from year to year in response to physical variability. Wetherall and Yong (1986) suggested that recruitment is independent of stock size over a wide range of stock sizes, and that interannual variability in recruitment is probably responsible for fluctuations in population size. This is supported in part by calculations of recruitment from Borets (1975; Table 1). One of the first suggestions of a mechanism for recruitment in seamount populations invoked the concept of stationary Taylor columns over seamounts for maintenance of pelagic larvae (Shomura and Barkley 1979). This is an extension of the ideas on the conservation of insular plankton described by Boden (1952). Others have suggested that seamount populations are derived from upstream source populations; the distances proposed have been as great as 1,100 nmi (Lutjeharms and Heydorn 1981b). This could be the case for the populations of *M. muelleri* on Hancock Seamount; large populations are present in waters of Japan (Okiyama 1981) and advection in the Kuroshio could bring them to the area of the seamount in 100-200 days (K. Mizuno, Tohoku Regional Fish. Res. Lab., Shiogama, Japan). Similar advective mechanisms may link the seamount population of alfonsin, *Beryx splendens*, to that in Japan.

Potential recruitment mechanisms must be a function of the physical oceanography and life histories of the species concerned. The physical oceanography of the SE-NHR region, including dominant effects of the North Pacific Current and the Kuroshio Extension, is complex (Fig. 1). The existence of eddies in the region has been discussed. As the currents impinge upon the Emperor Seamounts, there is a change in the hydrographic pattern, including major differences in dynamic height perturbations and current flow east as compared to west of the chain (Roden 1977; Roden et al. 1982). The region of the SE-NHR seamounts, however, is also in the subtropical Pacific front. This front is best developed from late fall to early summer (Roden 1980) and eddies are shed along the front (Roden 1981). Mizuno and White (1983) have demonstrated that interannual variations exist in the latitudinal position of the Kuroshio, and thus the position of the front, resulting in variability in eddy production. Further south, at lat. 20°-24°N, is the Subtropical Countercurrent, which could conceivably transport pelagic eggs and larvae back to Japanese waters (Uda 1970).

Whereas the effects of seamounts on large scale flow have been described, the smaller scale effects have been largely inferred due to the scale of sampling (Roden 1986). Flow perturbations in the regions of the seamounts suggest eddy formation, and indeed satellite-tracked drifters have become trapped in eddies over seamounts (Cheney et al. 1980; Richardson 1980; Lutjeharms and Heydorn 1981b). Current flow patterns over the seamounts may thus vary with seamount morphology, ocean current strength, and season.

From a biological standpoint, research must be initiated to fill important gaps in our knowledge of the life history and behavior of the species of interest. Larval, pelagic, juvenile (Borets 1979) and benthic adult pelagic armorhead and alfonsin have been captured, but distribution of the intervening stages is unclear; in any case, the pelagic young stages of both species are relatively rare.

experimental and commercial gear, which are notoriously poor for capturing juvenile stages. It is possible that younger specimens are recruited to the seamounts but are not available to our current sampling. Alfonsin may segregate to different habitats by age or size, as described by Seki and Tagami (1986). Submersible research could elucidate several aspects of the biology, habitat, and behavior of alfonsin and pelagic armorhead on the seamounts and allow a more comprehensive understanding of data collected using conventional shipboard methods. In several areas, for example, fish are apparently abundant in regions with high relief which prevent effective trawling operations (Yamamoto et al. 1978). Survey of these areas may allow more complete assessment of the populations and also provide information on the presence of juveniles and the nature of juvenile habitat (Uzmann et al. 1977; Carlson and Straty 1981).

Population age structure must also be determined. Based upon the ages determined in different studies, it is apparent that age validation work must be completed before a full study is undertaken. In armorhead, we must develop growth curves which will include the rare, larger specimens as well as curves based upon the dominant commercial sizes, which are apparently dominated by 2- and 3-year olds. Also, capture of the smallest specimens, whether in surface collections or from submersible benthic juvenile habitat will be necessary to aid our understanding of the growth dynamics; what percentage of somatic growth occurs before recruitment to seamounts? By considering the variability in age structure from year to year and the relationship with fish morphology, we may be able to estimate the variability in recruitment from year to year. If armorhead recruitment to seamounts occurs at later ages, as currently appears probable, then there are several points in the life history where variability in recruitment or year class strength could be influenced. Very strong recruitment, for example, apparently occurred in 1972 (Borets 1975; Takahashi and Sasaki 1977; Wetherall and Yong 1986). What is the role of recruitment variability in population abundance? Can we identify environmental features which may be responsible for recruitment variability? Physical and biological factors during the pelagic phase may play a role. Based on data from 11 years between 1969 and 1981 (in Humphreys et al. 1984), there is a negative correlation ($r = -0.77$) between catch per unit effort and mean length of armorhead. This suggests that density-dependent growth may occur in the pelagic environment.

Continued data collection will be necessary for population assessment. The fisheries-dependent model developed by Wetherall and Yong (1986) should be refined as more data become available and as the above research results allow better interpretation of existing data. Some level of continued fishing effort is desirable to allow model updating, stock monitoring, and development of biomass estimates. As ancillary goals, however, we should attempt some level of fisheries-independent resource assessment. At present, we have no ideas on changes in catchability that may have occurred through the history of the fishery. We should pay particular attention to methods such as hydroacoustic assessment, which could provide further information on the behavior of the species as well as fishery-independent assessment which could cover relatively large areas during daytime when the fish are unavailable to the trawl.

A major resource-related question concerns the trophic relationship of pelagic and demersal species. Preliminary work suggests that pelagic armorhead and alfonsin share similar prey resources. Is this resource base also common with the dominant pelagic species, including albacore, skipjack tuna, and squid? If so, have stocks of any of these potential competitors increased as pelagic armorhead stocks declined? The increased catch of alfonsin is suggested by Sasaki (1986) to reflect a change in targeted species by fishermen. We should also consider the speculation raised in the workshop discussion by Sasaki, namely, that pelagic armorhead use seamounts for spawning and that the "fat" condition developed in the pelagic environment deteriorates there due to lack of food. This speculation could be treated as a testable hypothesis, namely that insufficient food resources exist to maintain the virgin populations. An ecosystem model of a specific seamount would provide a means of addressing these issues.

The questions of seamount productivity should be addressed as a mechanistic phenomenon in a multidisciplinary fashion with key contributions from biological and physical oceanography. The general research question is "What are the factors important in maintaining large populations on seamounts?" This question should be addressed, as mentioned above, as one of productivity versus advection and convergence. Not all seamounts or banks would be classified as highly productive. Is the pattern of the SE-NHR seamounts a general phenomenon, with the energy simply channeled to other trophic levels or ecosystems, or are there specific features necessary for a highly productive seamount? If the latter is true, what are the features necessary to define a productive versus a nonproductive seamount? If we can define these features, it may be possible to describe areas in the sea where fisheries production may be unexpectedly high. The deep sea has traditionally been viewed as relatively low in production and biomass, but the development of the orange roughy fishery in New Zealand at depths from 800 to 1,200 m is currently providing an annual harvest in excess of 30,000 MT (Robertson and Grimes 1983). Thus knowledge of the factors important in productivity of deeper waters may aid in searching deepwater areas where resource exploration has not been conducted.

Research of this nature will require a variety of research disciplines. First, physical oceanographic studies based on closely spaced sampling grids as proposed by Roden (1986) will need to determine the conditions for development of eddies, Taylor columns, fronts, and other mesoscale features of flow complexity. Also, since we are interested in productivity effects in the euphotic zone, we must consider how these effects transfer into the mixed layer. Further research with moored current meter arrays, satellite- or radio-tracked drogues, and remote sensing will allow definition of the seasonal nature of variability in these mesoscale features. Are these features consistent within season, from year to year? What role is played by interannual variability of the kind described by Mizuno and White (1983)? Given the bottom topography and information on ocean currents, can one predict locations of eddies or gyres?

A variety of research on the biological oceanography of the water columns over seamounts is also of interest. What is the variability of primary productivity in the region of seamounts? Can a signal be detected in the levels of primary productivity associated with seamounts and if so, what is the residence time and consistency of such productivity? If enhanced productivity is present, however, further work will be necessary to demonstrate whether it is advected away or remains in the region for transfer to higher trophic levels of both fishes and benthos. Also, if there is no signal in primary productivity, can we assume that convergence and aggregation are responsible for seamounts with high biomass? As this question is considered, it should be related to areas other than seamounts, including banks (Uda and Ishino 1958), coastal headlands (Alldredge and Hamner 1980), and islands (Boden 1952; Hamner and Hauri 1981), where similar phenomena may occur.

Secondary productivity studies and descriptions of the spatial distribution and abundance of plankton and nekton will also be necessary. What is the mechanism of vertical flux of materials from surface waters to the seamounts? The dominant fish species of the SE-NHR seamounts apparently forage in the water column (Sakiura 1972; Borets 1979); is the mechanism of vertical transport a biologically mediated one? Do the benthos of seamounts show enrichment relative to shelf-slope biomass values, and if so, what is the energy source? We should undertake trophic studies which will allow better description of the ecosystem interactions in seamount regions. In this manner, preliminary models of the energy flow and higher trophic level production could be estimated. Does the combination of virgin stocks of demersal seamount populations and the pelagic populations require higher energy levels than average regional primary productivity would indicate? This may be a productive preliminary approach to assessing research questions on seamount oceanography.

In conclusion, seamounts represent an ocean feature whose potential for biological resources has been largely overlooked. Although seamounts may never represent a major contribution to world fishery resources, rational exploitation of the seamount resources requires a great deal of information before we can expect management to sustain populations. The armorhead is characterized by a broad feeding range, a wide variety of prey organisms, rapid growth, and early maturity. These features suggest that proper management of this resource could result in a significant, sustainable yield. The scientific questions associated with seamount oceanography and productivity are important to understanding the dynamics of seamount ecosystems.

CITATIONS

ALLDREDGE, A. L., and W. M. HAMNER.
1980. Recurring aggregations of zooplankton by a tidal current. Estuarine Coastal Mar. Sci. 10:31-37.

ANGEL, M. V., and M. J. R. FASHAM.
1983. Eddies and biological processes. *In* A. R. Robinson (editor), Eddies in marine science, p. 492-541. Springer Verlag, N.Y.

BACKUS, R. H., J. E. CRADDOCK, R. L. HAEDRICH, D. L. SHORES, J. M. TEAL, A. S. WING, G. W. MEAD, and W. D. CLARKE.
1968. *Ceratoscopelus maderensis*: Peculiar sound-scattering layer identified with this myctophid fish. Science (Wash. D.C.) 160:991-993.

BEZRUKOV, Y. F., and V. V. NATAROV.
1976. Formation of abiotic conditions over the submarine eminences of some regions of the Pacific Ocean. [In Russ.] Izv. Pac. Sci. Res. Inst. Fish. Oceanogr. (TINRO) 100:93-99. (Engl. transl. by W. G. Van Campen, 1983; available Southwest Fisheries Center Honolulu Laboratory, National Marine Fisheries Service, NOAA, Honolulu, HI 96822-2396.)

BODEN, B. P.
1952. Natural conservation of insular plankton. Nature 169:697.

BOEHLERT, G. W.
1985. Effects of Southeast Hancock Seamount on the pelagic ecosystem. [Abstr.] EOS, Trans. Am. Geophys. Union 66:1336.

BOEHLERT, G. W., and M. P. SEKI.
1984. Enhanced micronekton abundance over mid-Pacific seamounts. [Abstr.] EOS, Trans. Am. Geophys. Union 65:928.

BORETS, L. A.
1975. Some results of studies on the biology of the boarfish (*Pentaceros richardsoni* Smith). [In Russ.] Invest. Biol. Fish. Fish. Oceanogr. TINRO, Vladivostok 6:82-90. (Engl. transl. by W. G. Van Campen, 1984, 9 p., Transl. No. 97; available Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)
1979. The population structure of the boarfish, *Pentaceros richardsoni*, from the Emperor Seamounts and the Hawaiian Ridge. J. Ichthyol. 19(3):15-20.

CARLSON, H. R., and R. R. STRATY.
1981. Habitat and nursery grounds of Pacific rockfish, *Sebastes* spp., in rocky coastal areas of southeastern Alaska. Mar. Fish. Rev. 43(7):13-19.

CHENEY, R. E., P. L. RICHARDSON, and K. NAGASAKA.
1980. Tracking a Kuroshio cold ring with a free-drifting surface buoy. Deep-Sea Res. 27A:641-654.

CHIKUNI, S.
1971. Groundfish on the seamounts in the North Pacific. [In Jpn.] Bull. Jpn. Soc. Fish. Oceanogr. 19:1-14. (Fish. Res. Board Can. Transl. No. 2130.)

EIDE, L. I.
1979. Evidence of a topographically trapped vortex on the Norwegian continental shelf. Deep-Sea Res. 26:601-621.

FEDOSOVA, R. A.
1974. Distribution of some copepod species in the vicinity of the underwater Hawaiian Ridge. Oceanology 14:724-727.

FUJII, E.
1986. The zoogeographical features of fishes in the vicinity of seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 67-69. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

GENIN, A., and G. W. BOEHLERT.
1985. Dynamics of temperature and chlorophyll structures above a seamount: An oceanic experiment. J. Mar. Res. 43:907-924.

GRIFFITHS, F. B., and S. B. BRANDT.
1983. Mesopelagic crustacea in and around a warm-core eddy in the Tasman Sea off Eastern Australia. Aust. J. Mar. Freshwater Res. 34:609-623.

GRIGG, R. W.
1982. Precious coral in the Pacific; economics and development potential. INFOFISH Marketing Dig. 2:8-11.

HALL, M., and A. F. QUILL.
1983. Biological sound scattering in an ocean eddy. Aust. J. Mar. Freshwater Res. 34:563-572.

HAMNER, W. M., and I. R. HAURI.
1981. Effects of island mass: Water flow and plankton pattern around a reef in the Great Barrier Reef lagoon, Australia. Limnol. Oceanogr. 26:1084-1102.

HARDY, G. S.
1983. A revision of the fishes of the Family Pentacerotidae (Perciformes). N.Z. J. Zool. 10:177-220.

HOGG, N. G.
1980. Effects of bottom topography on ocean currents. *In* GARP Publication Series 23:167-205. WMO-ICSU.

HUGHES, S. E.
1981. Initial U.S. exploration of nine Gulf of Alaska seamounts and their associated fish and shellfish resources. Mar. Fish. Rev. 43 (1):26-33.

HUMPHREYS, R. L., Jr., and D. T. TAGAMI.
1986. Review and current status of research on the biology and ecology of pelagic armorhead. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 55-62. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

HUMPHREYS, R. L., Jr., D. T. TAGAMI, and M. P. SEKI.
1984. Seamount fishery resources within the southern Emperor-northern Hawaiian Ridge area. *In* R. W. Grigg, and K. Y. Tanoue (editors), Proceedings of the Symposium on Resource Investigations in the Northwestern Hawaiian Islands, Vol. 1, May 25-27, 1983, University of Hawaii, Honolulu, Hawaii, p. 283-327. UNIHI-SEAGRANT-MR-84-01.

HUPPERT, H. E.
1975. Some remarks on the initiation of inertial Taylor columns. J. Fluid Mech. 67:312-347.

HUPPERT, H. E., and K. BRYAN.
1976. Topographically generated eddies. Deep-Sea Res. 23:655-679.

INOUE, M.
1983. Exploitation of fishing grounds of southward migrants of fall skipjacks in the northwestern Pacific Ocean. [In Jpn., Engl. summ.] J. Fac. Mar. Sci. Tech., Tokai Univ. 17:121-130.

ISAACS, J. D., and R. A. SCHWARTZLOSE.
1965. Migrant sound scatterers: Interactions with the sea floor. Science (Wash. D.C.) 150:1810-1813.

LUTJEHARMS, J. R. E., and A. E. F. HEYDORN.
1981a. Recruitment of rock lobster on Vema Seamount from the islands of Tristan da Cunha. Deep-Sea Res. 28A:1237.

LUTJEHARMS, J. R. E., and A. E. F. HEYDORN.
1981b. The rock-lobster (*Jasus tristani*) on Vema Seamount: Drifting buoys suggest a possible recruiting mechanism. Deep-Sea Res. 28A: 631-636.

MIZUNO, L., and W. B. WHITE.
1983. Annual and interannual variability in the Kuroshio Current system. J. Phys. Oceanogr. 13:1847-1867.

MURPHY, G. I., and R. S. SHOMURA.
1972. Pre-exploitation abundance of tunas in the equatorial central Pacific. Fish. Bull., U.S. 70:875-913.

NELLEN, W.

1973. Untersuchungen zur Verteilung von Fischlarven und Plankton im Gebiet der Grossen Meteorbank (Investigations on the distribution of fish larvae and plankton near and above the Great Meteor Seamount.) Meteor Forschungsergeb. Reihe D-Biol. 13:47-69.

OKIYAMA, M.

1981. Abundance and distribution of eggs and larvae of a sternoptychid fish, *Maurolicus muelleri*, in the Japan Sea, with comments on the strategy for successful larval life. Rapp. P-V. Réun. Cons. Int. Explor. Mer 178:246-247.

OLSON, D. B., and R. H. BACKUS.

1985. The concentrating of organisms at fronts: a cold-water fish and a warm-core Gulf Stream ring. J. Mar. Res. 43:113-137.

OWEN, R. W.

1981. Fronts and eddies in the sea: Mechanisms, interactions, and biological effects. *In* A. R. Longhurst (editor), Analysis of marine ecosystems, p. 197-233. Acad. Press, N.Y.

OWENS, W. B., and N. G. HOGG.

1980. Oceanic observations of stratified Taylor columns near a bump. Deep-Sea Res. 27A:1029-1045.

PEREYRA, W. T., W. G. PEARCY, and F. E. CARVEY, Jr.

1969. *Sebastodes flavidus*, a shelf rockfish feeding on mesopelagic fauna, with consideration of the ecological implications. J. Fish. Res. Board Can. 26:2211-2215.

PRATT, R. M.

1967. Photography of seamounts. *In* J. B. Hersey (editor), Deep-sea photography, p. 145-158. Johns Hopkins Oceanogr. Stud. 3. Johns Hopkins Press, Baltimore.

RAYMORE, P. A., Jr.

1982. Photographic investigations on three seamounts in the Gulf of Alaska. Pac. Sci. 36:15-34.

RICHARDSON, P. L.

1980. Anticyclonic eddies generated near the Corner Rise seamounts. J. Mar. Res. 38:673-686.

ROBERTSON, D. A., and P. J. GRIMES.

1983. The New Zealand orange roughy fishery. *In* J. L. Taylor and G. G. Baird (editors), New Zealand finfish fisheries: The resources and their management, p. 15-20. Trade Publ. Ltd., Auckland. [Also Proceedings, Conference on New Zealand Fishery Resources.]

RODEN, G. I.

1970. Aspects of the mid-Pacific transition zone. J. Geophys. Res. 75:1097-1109.

1977. Long wave disturbances of dynamic height in the North Pacific. J. Phys. Oceanogr. 7:41-49.

1980. On the subtropical frontal zone north of Hawaii during winter. J. Phys. Oceanogr. 10:342-362.

1981. Mesoscale thermohaline, sound velocity and baroclinic flow structure of the Pacific subtropical front during the winter of 1980. J. Phys. Oceanogr. 11:658-675.

1986. Aspects of oceanic flow and thermohaline structure in the vicinity of seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 3-12. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

RODEN, G. I., B. A. TAFT, and C. C. EBBSEMEYER.

1982. Oceanographic aspects of the Emperor Seamounts region. J. Geophys. Res. 87:9537-9552.

ROYER, T. C.

1978. Ocean eddies generated by seamounts in the North Pacific. Science (Wash. D.C.) 199:1063-1064.

SAKIURA, H. (translator).

1972. The pelagic armorhead, *Pentaceros richardsoni*, fishing grounds off the Hawaiian Islands, as viewed by the Soviets (So-Ren kara mita Hawaii oki kusakari tsubodai gyojyo). [In Jpn.] Suisan Shuho (The Fishing & Food Industry Weekly) 658:28-31. (Engl. transl. by T. Otsu, 1977, 7 p., Transl. No. 17; available Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu, HI 96822-2396.)

SASAKI, T.

1986. Development and present status of Japanese trawl fisheries in the vicinity of seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 21-30. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

SEKI, M. P., and D. T. TAGAMI.

1986. Review and present status of handline and bottom longline fisheries for alfonsin. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 31-35. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

SHOMURA, R. S., and R. A. BARKLEY.

1979. Ecosystem dynamics of seamounts—a working hypothesis. *In* Proc. 4th Symp. Co-op. Study of the Kuroshio and Adjacent Regions, p. 789-790. Saikon Publ. Co., Tokyo, Japan.

SMITH, W. G., and W. W. MORSE.

1985. Retention of larval haddock *Melanogrammus aeglefinus* in the Georges Bank region, a gyre-influenced spawning area. Mar. Ecol. Prog. Ser. 24:1-13.

SMOOT, N. C.

1985. Guyot and seamount morphology and tectonics of the Hawaiian-Emperor elbow by multi-beam sonar. Mar. Geol. 64:203-215.

SUNDBY, S.

1984. Influence of bottom topography on the circulation at the continental shelf off northern Norway. Fiskeridir. Skr. Ser. Havunders. 17:501-519.

TAKAHASHI, Y., and T. SASAKI.

1977. Trawl fishery in the central North Pacific seamounts (Kita Taiheiyo chubu kaizan ni okeru tororu gyogyo). Northern waters groundfish fishery—data (3) (Hokuyo soko-uo gyogyo—Shiryo (3)). [In Jpn.] Div. Northern Waters Groundfish Resour., Far Seas Fish. Res. Lab., 45 p. (Engl. transl. by T. Otsu, 1977, 49 p., Transl. No. 22; available Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu HI 96822-2396.)

TAYLOR, G. I.

1917. Notion of solids in fluids when the flow is not irrotational. Proc. R. Soc. Edinb. Sect. A93:99-113.

UDA, M.

1970. Fishery oceanographic studies of frontal eddies and transport associated with the Kuroshio system including the "subtropical countercurrent." *In* J. C. Marr (editor), The Kuroshio, p. 593-604. East-West Center Press, Honolulu.

UDA, M., and M. ISHINO.

1958. Enrichment pattern resulting from eddy systems in relation to fishing grounds. J. Tokyo Univ. Fish. 44:105-129.

UZMANN, J. R., R. A. COOPER, R. B. THEROUX, and R. L. WIGLEY.

1977. Synoptic comparison of three sampling techniques for estimating abundance and distribution of selected megafauna: Submersible vs camera sled vs otter trawl. Mar. Fish. Rev. 39(12):11-19.

VASIL'KOV, V. P., and L. A. BORETS.

1978. Determining the age of boarfishes by spectrophotometric analysis of scale structure. Sov. J. Mar. Biol. 4(1):545-548.

WETHERALL, J. A., and M. Y. Y. YONG.

1986. Problems in assessing the pelagic armorhead stock on the central North Pacific seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 73-85. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

YAMAMOTO, K.

1986. A review of the fishery and catch per cruise for alfonsin stocks in the vicinity of Izu islands. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 87-91. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

YAMAMOTO, S., K. ISHII, S. SASKI, and T. MEGURO.

1978. Outlines of fisheries investigation on the Emperor Seamounts by the RV *Hokusei Maru* in 1977 and some technical problems. [In Jpn.] Bull. Jpn. Soc. Fish. Oceanogr. 33:56-64. (Engl. transl. by T. Otsu, 1984, 24 p., Transl. No. 91; available Southwest Fish. Cent., Natl. Mar. Fish. Serv., NOAA, Honolulu HI 96822-2396.)

YASUI, M.

1986. Albacore, *Thunnus alalunga*, pole-and-line fishery around the Emperor Seamounts. *In* R. N. Uchida, S. Hayasi, and G. W. Boehlert (editors), Environment and resources of seamounts in the North Pacific, p. 37-40. U.S. Dep. Commer., NOAA Tech. Rep. NMFS 43.

Humphreys et al. (1984) have described the current knowledge on life histories of pelagic armorhead and alfonsin. Young alfonsin apparently are recruited to the seamounts at an age of approximately 1 year after a pelagic larval stage (Chikuni 1971). It has been suggested that pelagic armorhead are recruited to seamounts after a largely pelagic existence, but the duration of this period is in question. Soviet scientists have suggested that recruitment to the seamounts occurs at an age of 6-9 years (Vasil'kov and Borets 1978), whereas the Japanese suggested that recruitment occurs at ages of 4-5 (Chikuni 1971). These ages were determined from different methods of scale reading. Our best estimates of age at recruitment for more recent samples suggest ages of 2-3 years, and the majority of recruits are 2-year olds (J. H. Uchiyama, Southwest Fish. Center Honolulu Lab.). All of these samples, however, have been taken with sampling gear for larger fish; virtually no sampling has been conducted on the seamounts which would collect small juveniles of either species. The recent discovery of large scale nursery areas for juvenile rockfish, *Sebastes* spp., in untrawlable areas in the coastal waters of Alaska required the use of a research submersible (Carlson and Straty 1981). In situ observation from a submersible, photographic transects, or other unconventional sampling techniques may thus be necessary to assess the presence and abundance of these important life history stages and to allow a fuller understanding of the recruitment process.

Knowing the duration of the pelagic period will allow better suggestions of recruitment mechanisms. The recruitment mechanism using Taylor columns as suggested by Shomura and Barkley (1979), for example, would probably require a relatively short-lived pelagic dispersal stage but could result in localized stocks or populations on individual seamounts. Eide (1979) noted trapped eddies over banks on the continental shelf off Norway, and Sundby (1984) suggested that these features allow retention of pelagic cod eggs and larvae sufficiently long for recruitment. A similar mechanism has been suggested for Georges Bank (Smith and Morse 1985). Alternatively, some species may have very extensive pelagic dispersal stages with different recruitment mechanisms, thus resulting in mixed stocks. Lutjeharms and Heydorn (1981b) suggested that rock lobster, *Jasus tristani*, is recruited to Vema Seamount after 9 months of pelagic drifting over some 1,100 nmi. Despite the long distance over which recruitment occurs, however, the mechanism is sufficiently robust to allow large-scale recruitment of depleted populations in relatively short periods of time (Lutjeharms and Heydorn 1981a).

The geographic distribution of a species may often provide an idea of the length of larval life and dispersal capabilities. Pelagic armorhead have now been divided to Northern and Southern Hemisphere species (*Pseudopentaceros wheeleri* and *P. richardsoni*, respectively; Hardy 1983). *Pseudopentaceros wheeleri* has been captured throughout the North Pacific (Fujii 1986) but is abundant only in localized regions such as the SE-NHR seamounts. The presumed long pelagic period of this species (2-3 years) allows such long-range dispersal but calls into question the mechanism of recruitment to the population centers. It may be that the physical factors responsible for enhancing productivity or aggregating prey over seamounts may also provide clues to their locations. If our interpretation of the long pelagic period is correct, it is probable that a single stock exists on the seamounts, as preliminary electrophoretic results suggest.

It is of interest to note that the orange roughy, *Hoplostethus atlanticus*, another deepwater fishery species, has a distribution pattern analogous to that of the pelagic armorhead (Robertson and Grimes 1983). Thus effects associated with other topographic features such as banks and islands (Uda and Ishino 1958) should also be investigated.

FUTURE RESEARCH DIRECTIONS

I will divide my suggestions of future research to those addressing strictly resource-associated questions and those of a more general nature dealing with mechanistic questions. The latter research areas, which I would define as relating to the general phenomena of high productivity or enrichment over seamounts, are generally beyond the logistic and financial contraints of the resource agencies and will need to be approached on a larger, multidisciplinary scale. The resource questions, although related, by necessity take a somewhat narrower approach, using available research vessels and fisheries data.

Research related to the resource issues must address the basic questions necessary for management of the fishery and will require a combination of research on stock structure, reproduction and behavioral biology, life history, and population assessment. Research on stock structure and species separation (particularly for *Pseudopentaceros*) should begin immediately to complete the preliminary work done and to allow interpretation and planning of other work. The research design should include work on pelagic armorhead and alfonsin. For pelagic armorhead, the questions include stock differences among seamounts (which preliminary electrophoretic information suggests do not differ), between fat and lean types, and between benthic and pelagic groups. It would also be of interest to compare Northern and Southern Hemisphere specimens to aid in our understanding of the taxonomic issues and species descriptions recently published by Hardy (1983). For the alfonsin, no work has been conducted to date on stock differentiation, but it would be interesting to determine if stock differences exist among seamounts and also the relationship of seamount and the western Pacific populations described by Yamamoto (1986). The apparent transport of Japanese sardine, *Sardinops melanosticta*, to the Emperor Seamounts (Yasui 1986), provides a mechanism for transport of early life stages of alfonsin from Japanese waters to the seamount region.

As described above, a wide variety of research on life history and biology of the dominant species will be of interest. The conceptual model of pelagic armorhead life history proposed by Humphreys and Tagami (1986), for example, has many unknowns which could be tested. Another key area of interest will be a study of the spawning and early life history of the two dominant species. Pelagic armorhead spawn during winter, alfonsin during summer. Do the larval distributions differ in response to the seasonal differences in physical oceanography? Can larvae be captured in sufficient numbers to meaningfully describe the effects of currents on distribution and dispersion? Plankton surveys should be conducted which consider the vertical distribution as it relates to water column structure and horizontal distribution as it relates to the seamounts and current flow patterns. What are the recruitment strategies of these two species? Is recruitment seasonal, as is spawning? Is the Taylor column concept realistic as a mechanism for the maintenance of pelagic populations? Many of these questions can only be addressed with the help of sophisticated analysis of physical oceanography to support our understanding of the biological oceanography.

Research must also be conducted to develop a better understanding of the habitat on the seamounts and the behavior of the dominant species. What is the diel activity pattern of each species? Our current ideas of the age at recruitment are based upon captures in