Populations of the Sternoptychid Fish *Maurolicus muelleri* on Seamounts in the Central North Pacific[1]

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ABSTRACT: The lightfish, *Maurolicus muelleri* (Gmelin), is a cosmopolitan sternoptychid fish most abundant near continental shelf-slope breaks and rare in the open ocean. Recent studies have documented dense populations on seamounts of the South Atlantic and North Pacific. At Southeast Hancock Seamount, a small guyot in the central North Pacific, *M. muelleri* populations are mainly composed of juveniles. Seasonal length frequencies suggest that recruitment at sizes greater than 20 mm standard length (SL) occurs principally in spring and summer months, with growth over summer and fall coincident with decreasing abundances. Mature fish in reproductive condition occur in winter months but do not survive to the following spring; they also may be too few at this small seamount to support annual recruitment. Potential sources of additional recruitment include populations at several larger seamounts in the southern Emperor group and also the large populations around Japan. Advection of eggs and larvae in the Kuroshio Extension may provide recruits for dependent populations at the seamounts. Mean current flow and satellite-tracked drifters suggest a transit time of 100–200 days from the coast of Japan to the region of the seamounts; estimates of age at length suggest that smaller fish have similar ages at recruitment. Gill-raker counts, however, differ between Japanese and seamount populations. We suggest that the southern Emperor Seamount populations serve as the source for replenished annual recruitment to the small population at Southeast Hancock Seamount.

THE LIGHTFISH, *Maurolicus muelleri* (Gmelin), occurs in high abundance near continental slopes in the Southeast Pacific (Robertson 1976, Clarke 1982), the Northwest Pacific near Japan (Okiyama 1971), the South Atlantic (de Ciechomski 1971, Hulley and Prosch 1987), and the Northeast Atlantic (Gjosaeter 1981). Its high biomass and shoaling behavior have suggested fishery potential in some areas

(Clarke 1982, Prosch and Shelton 1983), and it serves as an important prey source for many predatory fishes (Okiyama 1971). Although a member of a principally oceanic, mesopelagic family, the species seems to be associated with land masses, spending daylight hours near the bottom at depths from 100 to 500 m and rising into shallow water in large shoals at night where it apparently feeds (Okiyama 1971, Robertson 1976, Kawaguchi and Mauchline 1987).

This species is rarely reported in open ocean areas, but the characteristic eggs may be common over oceanic depths adjacent to population centers (Williams and Hart 1974). In large-scale midwater trawl surveys away from land, however, *M. muelleri* is rarely encountered (Barnett 1984), but some records of small juveniles exist (Mukhacheva 1981, Clarke 1984). Drift in ocean currents can

result in colonization of new habitats and range extensions for this species (Borokin and Grigorev 1987).

In the North Pacific, *M. muelleri* is generally limited to the western half, with no records from the eastern North Pacific (Mukhacheva 1981). Two population centers of *M. muelleri* are present in Japan. The greatest density occurs in the Sea of Japan, where the population biomass may exceed 3 million metric tons (Okiyama 1981). A smaller population occurs along the Pacific coast of southern Japan (Okiyama 1971). Other specimens have been encountered in the central North Pacific as stomach contents of whales (Kawamura 1973). More recently, large numbers have been reported from relatively isolated seamounts, both in the North Pacific (Borets and Sokolovsky 1978, Borets 1986, Boehlert 1988) and South Atlantic (Linkowski 1983). In this paper we describe certain aspects of the population of *M. muelleri* at Southeast Hancock Seamount, an isolated oceanic seamount at the northern end of the Hawaiian Ridge, and consider the origin and persistence of this population and its potential biogeographic relationship to larger populations elsewhere in the North Pacific.

MATERIALS AND METHODS

Observations were made from the NOAA vessel *Townsend Cromwell* during seven cruises (July 1984, February and July 1985, September and November 1986, April 1987, and July–August 1988) to Southeast Hancock Seamount (29° 48′ N lat., 179° 04′ E long.). The 1988 cruise extended northwestward to the southern Emperor Seamounts, including Colahan (31° 02′ N lat., 175° 54′ E long.), Kammu (32° 10′ N lat., 173° 00′ E long.), and Koko (35° 00′ N lat., 171° 30′ E long.) seamounts. Collections of *M. muelleri* were made with a 1.8-m Isaacs-Kidd midwater trawl (IKMT) with a 3-mm mesh body and a cod end of either 3-mm or 0.505-mm mesh towed at 150–200 cm/sec; volumes filtered with this net were estimated using mechanical flowmeters. Other samples were taken with a larger square midwater herring trawl (mouth

area ca. 50 m²) with 6-mm cod end mesh. When fish densities were estimated, only the IKMT hauls were considered. The scattering layer was also observed with a Simrad EQ-38 echosounder operating at 38 kHz. Specimens were preserved at sea in 10% buffered formalin. Subsamples from September 1986 and April 1987 cruises were preserved in 70% ethanol for later examination of otoliths. Standard lengths were measured to the nearest 0.1 mm using a dial caliper. Statistical comparison of length frequencies was accomplished using the nonparametric Kolmogorov-Smirnov test.

In the laboratory, *M. muelleri* was sorted from samples. Sex of specimens with developing gonads was determined according to Gjosaeter (1981) and Yuuki (1982), and standard length (SL) was measured. Otoliths were examined for age determination with techniques following Gjosaeter (1981); presumptive daily increments on whole otoliths mounted on microscope slides were counted under a compound microscope. Otolith radii measurements were made with a dissecting microscope following Yuuki (1984). Total gill rakers were counted on the first gill arch.

A 150-kHz vessel-mounted acoustic Doppler current profiler (ADCP) was used to measure currents in 1988 while the vessel was over three seamounts of the southern Emperor–northern Hawaiian Ridge. Techniques for ADCP data processing generally followed Wilson and Boehlert (1990). Reported current speeds were depth averaged over 40–210 m.

RESULTS

In the North Pacific, *Maurolicus muelleri* populations occur principally in the western region; in the central North Pacific, specimens have been captured at several seamounts between lat. 29° 48′ and 38° 40′ N (Mukhacheva 1981, Borets 1986; this study, Figure 1). Open ocean records are relatively few. Examination of published and unpublished collection records revealed few occurrences that are not in the vicinity of the seamounts marked in Figure 1. The westernmost specimens taken were eggs (T. Watanabe, Tohoku Regional Fish-
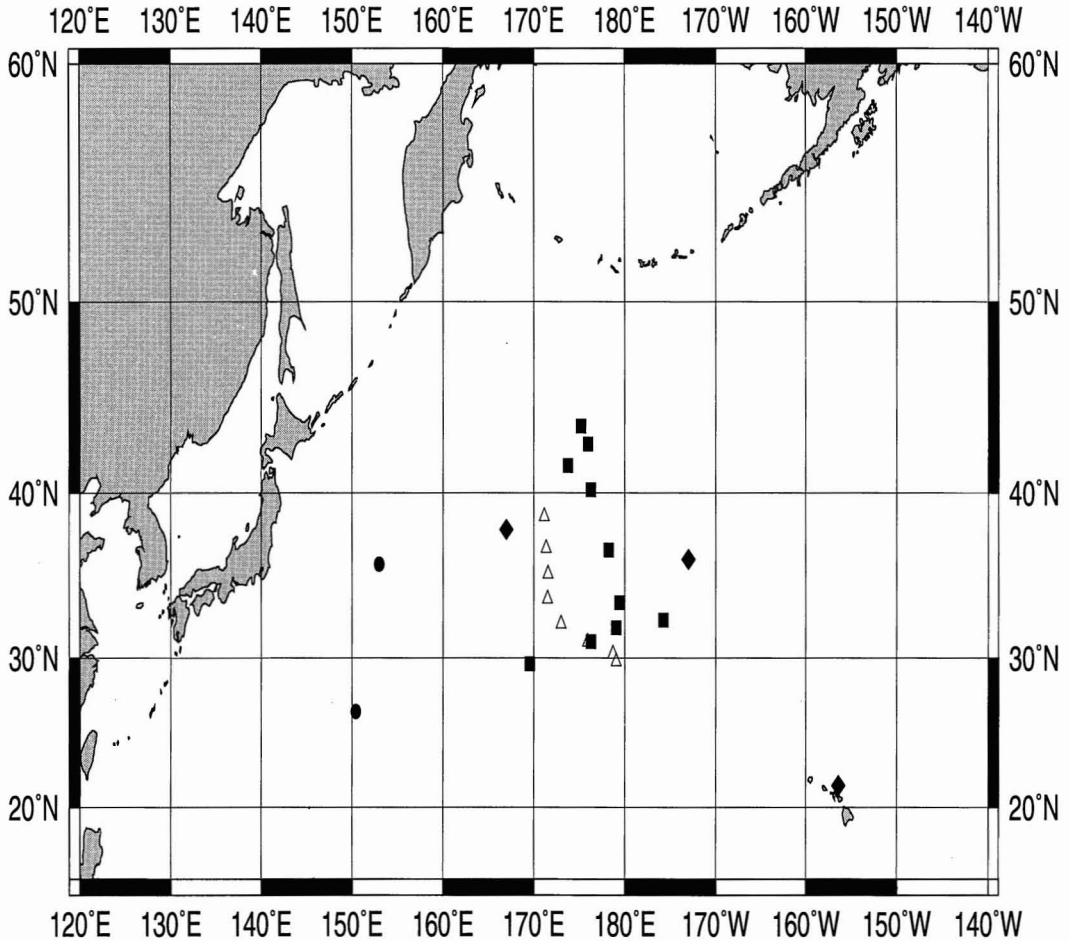
FIGURE 1. Distribution of *Maurolicus muelleri* in the North Pacific. Open triangles represent the locations of seamounts where *M. muelleri* occurs in topography-associated populations (Borets 1986; this study). Circles represent eggs taken in midwater trawl samples (T. Watanabe, Tohoku Regional Fisheries Laboratory, pers. comm.). The diamond west of the dateline represents a juvenile from a midwater trawl collection; that east of the dateline the stomach contents of a fish taken on a longline (R. H. Rosenblatt, Scripps Institution of Oceanography, pers. comm.). Squares represent records from the stomachs of sei and Bryde's whales (Kawamura 1973). The diamond off the main Hawaiian Islands represents data from Reid et al. (1991).

eries Research Institute, pers. comm.) and one juvenile from a midwater trawl survey (R. H. Rosenblatt, Scripps Institution of Oceanography, pers. comm.). Additional collection records from Scripps Institution of Oceanography indicate another from the stomach of a lancetfish, *Alepisaurus borealis* (= *ferox* Lowe), taken on longline over deep water east of the seamount chain (Figure 1; Rosenblatt, pers. comm.). Records from the Hokkaido University Museum of Zoology (K. Amaoka, pers. comm.) show specimens taken at Kinmei Seamount from stomach contents of the mirror dory, *Zenopsis nebulosa* (Temminck & Schlegel), a species known to be abundant at the seamounts (Borets 1986). North and east of the southern Emperor Seamount–associated populations (Figure 1), large numbers were taken in stomach contents of whales (Kawamura 1982). Finally, the

most southeasterly occurrence in the North Pacific is in the main Hawaiian Islands (Reid et al. 1991).

Because of the infrequent cruises to Southeast Hancock Seamount, insufficient seasonal length data were collected from any single year to assess modal progressions. Thus, to consider changes in length frequency across seasons, data from 1984 to 1987 were combined. Median lengths were different among seasons of the year (Figure 2): the smallest individuals, about 23 mm SL, were captured in spring; median size increased over the year, with the largest fish captured in winter. Although we have not comprehensively sampled throughout a single year, the unimodal nature

of the seasonal data and the lack of larger animals in spring and summer suggest an annual population with no evidence for a second year of life at Southeast Hancock Seamount. Fish at the seamount attain reproductive status, however, as shown by the presence of reproductively mature animals in winter collections (Wilson 1992) and by *M. muelleri* larvae taken in ichthyoplankton collections in winter (but not summer) collections (Boehlert and Mundy 1992); this is consistent with spawning in winter time when larger, reproductive animals are present.

Otoliths were analyzed from 22 specimens collected in late summer 1986 and 21 from spring 1987. They ranged from 26 to 43 mm SL (mean, 35.4), with otolith radii ranging from 0.55 to 0.70 mm. Gross examination under a dissecting microscope failed to reveal an annulus on any otolith. Examination of mounted otoliths under a compound microscope demonstrated clear increments presumed to represent daily growth. Counts of the increments from these fish ranged from 80 to 162, with an average of 119. Because of the narrow range of length and age, we fit no growth curve to the data, but length at age suggests that growth was more rapid than observed in Japan (Figure 3).

Gill rakers were counted from 86 specimens from Southeast Hancock Seamount taken in 1986, from 78 specimens from the stomachs of 11 sei and Bryde's whales (capture locations as in Figure 1), and from 28 specimens from the Pacific coast of Japan (including data from 12 specimens in Mead and Taylor [1953]). The gill-raker counts of seamount fish and those from whale stomachs (taken east of the seamounts) ranged from 26 to 32 (Figure 4). Counts from specimens from Japan were uniformly lower, ranging from 23 to 26; overlap in gill-raker numbers was minor between Japanese and central North Pacific specimens.

Midwater trawl samples were taken in August 1988 at three of the southern Emperor Seamounts northwest of Southeast Hancock. A total of 20 hauls captured 637 *M. muelleri*, both above and southwest of the seamount summits (Table 1). Length frequencies measured for 567 of these fish are different from
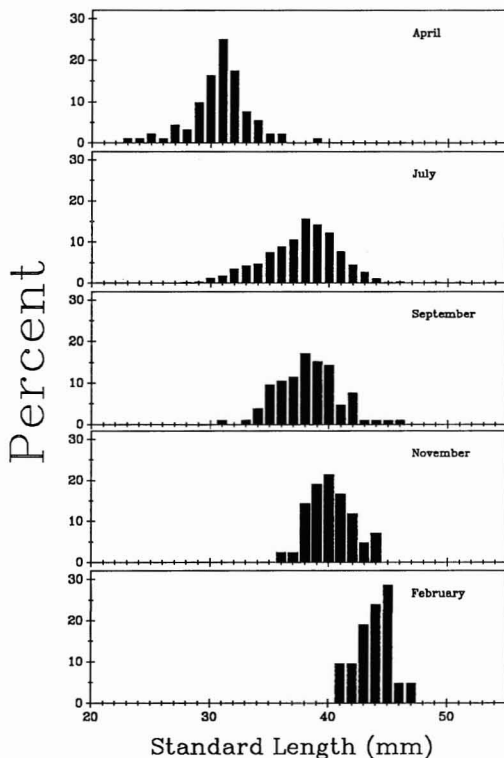

FIGURE 2. Seasonal length-frequency distributions of *Maurolicus muelleri* from Southeast Hancock Seamount. Samples were taken in different years and combined by month, as follows: April 1987, *n* = 92; July 1984, *n* = 352; July 1985, *n* = 654; September 1986, *n* = 105; November 1986, *n* = 42; February 1985, *n* = 21.
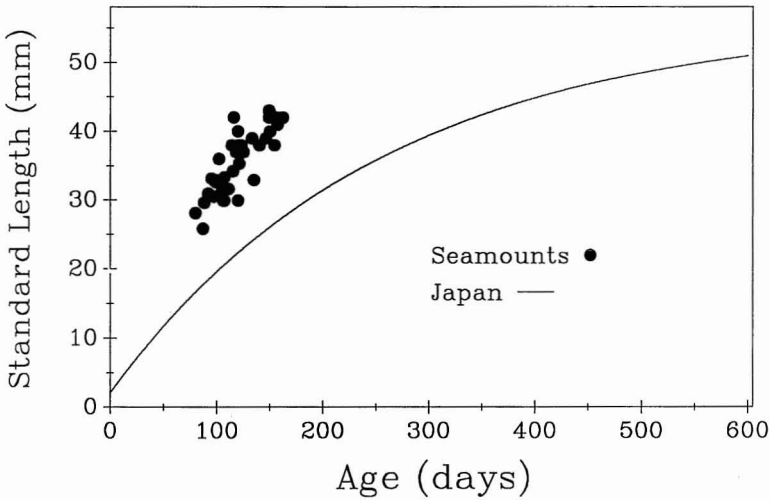
FIGURE 3. Age and growth of *Maurolicus muelleri* from Southeast Hancock Seamount. Age of specimens was determined using daily growth increments; age-length data points from this study are shown as circles. For comparison, the growth curve from spring-spawned fish from the Sea of Japan (Yuuki 1982) is indicated as a solid line.
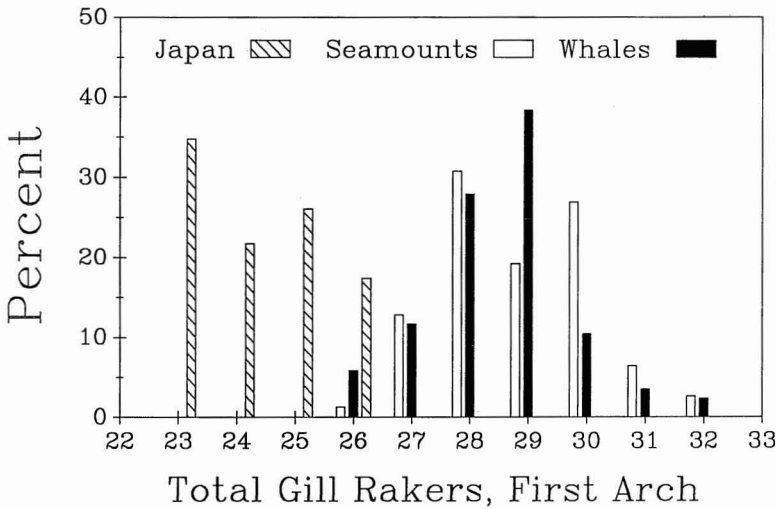

FIGURE 4. Gill-raker counts from *Maurolicus muelleri* from three capture locations. Specimens are from the Pacific coast of Japan (crosshatched bars, $n = 28$; M. Okiyama, pers. comm.; Mead and Taylor 1953), Southeast Hancock Seamount (open bars, $n = 86$), and the stomachs of sei and Bryde's whales (solid bars, $n = 78$).

those for 414 fish at Southeast Hancock Seamount taken on the same cruise (K-S test, $P < 0.01$), with slightly larger fish at Southeast Hancock (median, 34 versus 35 mm SL). Densities of fish taken at distances from 10 to 40 km southwest of the southern Emperor Seamount summits were ca. 10-fold less than over the summits (Table 1). Also, the length frequencies differed from those taken above the summit (K-S test, $P < 0.01$; Figure 5),

TABLE 1

Isaacs-Kidd Midwater Trawl Hauls Taken over the Southern Emperor Seamounts

SEAMOUNT	LOCATION	NO. OF TOWS	NO. OF *M. muelleri*	DENSITY $(10^{-5}\ m^{-3})$
Colahan	Summit	3	11	1.433
	Southwest	2	0	0.000
Kammu	Summit	3	543	68.933
	Southwest	4	53	5.300
Koko	Summit	4	27	2.725
	Southwest	4	3	0.300

NOTE: "Summit" tows were taken over the seamount summits; "Southwest" tows were taken at distances of 5 to 40 km (mean, 19 km) to the southwest of the summits. Average volumes filtered per tow were 25,000 m³.
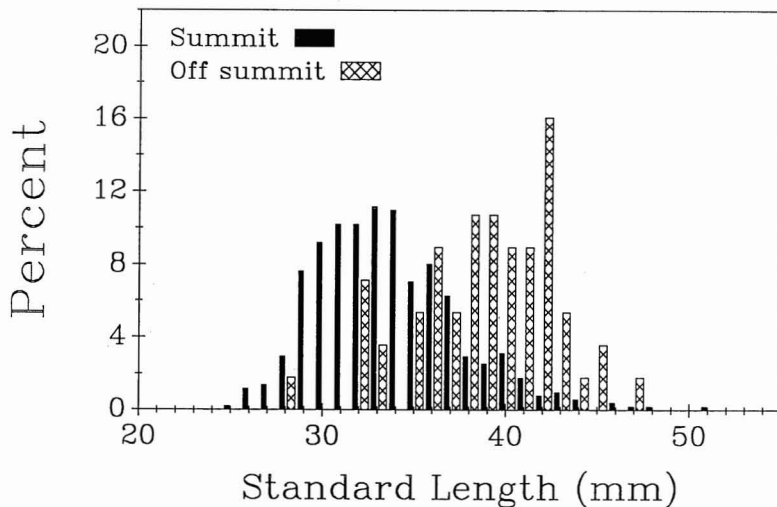

FIGURE 5. Length-frequency distributions of *Maurolicus muelleri* taken in August 1988 at the southern Emperor Seamounts. Data from fish captured over the seamount summits ($n = 511$) are contrasted with those taken at distances varying from 10 to 40 km southwest of the summits ($n = 56$).

with median sizes of 33 and 39 mm SL on and off the summit, respectively. Length frequencies of fish taken off the summit were also significantly larger than those of fish taken at Southeast Hancock on the same cruise.

Different current patterns were observed over each of the southern Emperor Seamounts visited during the 1988 cruise. Strong (31 cm/sec), generally northward currents were present over Colahan Seamount. At Kammu Seamount, currents were relatively weaker (14 cm/sec) and generally to the east-southeast. Currents over Koko Seamount were very weak (6 cm/sec), to the southeast initially but later flowed primarily northward.

DISCUSSION

Populations occurring on seamounts are often small because of very limited habitat. As with island populations, local extinction may occur periodically and reestablishment of populations depends upon recruitment from other sources (MacArthur and Wilson 1967, Choat et al. 1988). In the South Atlantic, for

example, the rock lobster *Jasus tristani* Holthuis recruits in large numbers to Vema Seamount from an insular source population some 2000 km away (Lutjeharms and Heydorn 1981*a,b*). Populations of *M. muelleri* exist on some South Atlantic seamounts in densities as high as 147 g/m² (Kalinowski and Linkowski 1983). Because specimens on most of these seamounts are immature (Linkowski 1983), it is likely that they are advected from populations near Argentina and Tristan da Cunha Island. Such populations fit the description of "dependent populations," which require separate, independent populations for replenishment. Dependent populations have been described in the North Pacific. Vasilenko and Sokolovskaya (1989), for example, described marked range extensions of populations of the black filefish, *Navodon modestus* (Günther), and horse mackerel, *Trachurus japonicus* (Temminck & Schlegel), into open ocean areas of the northwestern Pacific and suggested that the distribution extended to the region of the Emperor Seamounts. Belyayev (1990) developed this idea further and showed that the mackerel populations originated from the same stock; he suggested that a minimum population size of 2.7 million metric tons in the "independent," or source, population is necessary to support dependent populations at the seamount. Biomass estimates of *M. muelleri* in the Sea of Japan are on the order of 3 million metric tons (Okiyama 1981).

Although the Southeast Hancock Seamount population of *M. muelleri* was a consistent feature of our sampling over several years, it is difficult to determine whether or not it is a self-sustaining population. Midwater trawl samples and acoustic observations suggest a strong seasonality in abundance. Generally, abundances are greatest in summer, lowest in winter, and intermediate in fall based upon acoustic data (Wilson 1992). In late July 1984, densities exceeded four individuals per 1000 m³, whereas in winter 1985 abundance was less than 0.2 individuals per 1000 m³ (Boehlert 1988). The reduction in abundance could result from either natural mortality or advection away from this small seamount. Length-frequency patterns of *M.*

muelleri at Southeast Hancock Seamount (Figure 2) suggest that recruitment occurs in spring and summer months. The annual nature of the population, the low abundance in winter months, and the absence of fish in the size range between small larvae and 23 mm SL juveniles suggest that recruitment may depend upon an upstream source.

We examined evidence for two possible source populations, those in Japan and those on the southern Emperor Seamounts. Large populations of *M. muelleri* occur in coastal waters of Japan (Okiyama 1971), and a great deal of evidence exists for the advection of coastal fauna from Japan to waters of the central Pacific under the influence of the Kuroshio and Kuroshio Extension. Tropical-reef fish from the south of Japan have been captured at the northern end of the Hawaiian chain (Ralston 1981), and several species of fish in Hawaiian waters share a close affinity to the subtropical and temperate fish fauna of southern Japan (Hobson 1984). From central Japan, a variety of coastal pelagic species are advected to mid-Pacific waters. In many years, Japanese sardine, *Sardinops melanosticta* (Temminck & Schlegel), is a major prey item of albacore captured at the Emperor Seamounts (Yasui 1986). Similarly, juvenile *S. melanosticta*, *Engraulis japonica* Temminck & Schlegel (anchovy), *Scomber japonicus* Houttuyn (mackerel), and *M. muelleri* are major fish components of the diet of sei whales in the vicinity of the seamounts (Kawamura 1973). With the exception of *M. muelleri* described in Wilson (1992), no spawning populations of these species have been identified in the southern Emperor–northern Hawaiian Ridge seamount region. Although *S. japonicus* apparently has mechanisms for population maintenance in Japanese waters (Watanabe 1970), larvae and juveniles are often captured at considerable distances from shore, typically in years that result in poor year class strength (Belyayev 1985); thus the magnitude of this faunal advection may vary interannually, possibly with the strength of transport of the Kuroshio.

Ocean currents could conceivably advect *M. muelleri* from populations in both the Sea of Japan and the Pacific coast of Japan to

the region of Southeast Hancock Seamount. From the southern coast of Japan advection to the region of the seamounts (near 180° E long.) would take ca. 100 days given the mean current speed of the Kuroshio Extension (ca. 50 cm/sec). This time scale is supported by trajectories of satellite-tracked drifters deployed in the Kuroshio near Japan, which typically reach the region of the seamounts in periods of 100 to 200 days (Cheney et al. 1980). For the population in the Sea of Japan, Okiyama (1981) suggested that the major spawning was associated with flow of the warm Tsushima Current, which flows northward. Long-term mean flows of about 10 cm/sec suggest that eggs and larvae entrained in this current would take about 70 days to drift from Toyama Bay to the Tsugaru Strait. The Tsugaru Warm Current (TWC), which could carry the eggs, larvae, or juveniles between Honshu and Hokkaido, enters the Pacific and directs to the south (Kawai 1972). The modified TWC water could be entrained into the Kuroshio Extension near the Joban area; the transit in this case would take some 60 days. After entrainment, the path would be similar to that of the Pacific coast population and thus the total time to reach the seamount from the Sea of Japan would be 230 to 330 days.

Our biological results, however, do not strongly support a Japanese origin for the fish taken at Southeast Hancock Seamount. The distribution of ages (Figure 3) suggests that at least the smallest recruits are too young to have been advected from the Sea of Japan populations, because animals at the apparent recruitment size are on the order of 80–120 days of age (we cannot rule out recruitment of older, larger fish later in the summer, however). Advection from the Pacific coast of Japan is possible in this time frame. The length-frequency distributions from Southeast Hancock Seamount, when compared with those from Japan, are reminiscent of the situation in the South Atlantic, where Linkowski (1983) observed large, mature populations with 1- to 3-year-old animals in the westernmost area sampled but only unimodal juvenile populations (to 47 mm SL) in the downstream seamount populations. Borokin

and Grigorev (1987) observed a range extension of several hundred kilometers for *M. muelleri* in the Barents Sea and attributed it to enhanced transport of the Norwegian Current combined with a strengthening of the Murmansk Current; thus, advection may be a common pattern in the life history of this species.

Several biological features, however, differ between the seamount and Japanese populations. Length-frequency distributions of seamount populations are unimodal and only reach 1 yr of age, contrasting with the multimodal, multiyear size and age distributions reported in Yuuki (1982, 1984). Although the otolith radius–standard length relationship does not differ, no annuli were observed on seamount fish. This may be related to the seasonality of collection of the specimens (spring and fall), but there is little difference between summer and winter temperatures at Southeast Hancock Seamount at the depths inhabited by *M. muelleri* (Boehlert 1988). Growth of *M. muelleri* at the seamounts was much faster than that of spring-spawned fish from the Sea of Japan (Figure 3) and more similar to early growth rates noted by Linkowski (1983) in the South Atlantic. A similar situation exists in the North Atlantic, where populations in the Rockall Trough live only 1 yr (Kawaguchi and Mauchline 1987), contrasted with Norwegian populations living 3 yr (Gjosaeter 1981). In the Pacific example, this may be related to higher temperatures and enhanced foraging conditions in the region of the seamount, where oceanic zooplankton represent the major diet item (Hirota and Boehlert 1985). The smaller population size at Southeast Hancock Seamount compared with those on continental slopes may combine with abundant, advected oceanic prey to create an optimal feeding environment (Isaacs and Schwartzlose 1965) and thus more rapid growth. Like growth, gill-raker counts differ between the Southeast Hancock and Japanese populations as well.

The second potential source of recruitment at Southeast Hancock Seamount is from the southern Emperor Seamounts (north of 32° in Figure 1). The biology of these populations has not been described in detail; biological

characteristics of the Southeast Hancock and southern Emperor Seamount populations are more similar. The range of lengths in summer show little difference (Figures 2, 5). Gill-raker counts of *M. muelleri* from both Southeast Hancock Seamount and whale stomachs (Figure 4) agree with the counts from Mukhacheva (1981) for the southern Emperor Seamounts. They are considerably greater than counts from Japanese populations from either the Sea of Japan (Grey 1964, Okiyama 1971) or the Pacific coast (Figure 4). Although number of gill rakers is a flexible character in fish (McCart and Andersen 1967, Lindsey 1988), it is unknown whether this indicates genetic, population-level differences or variation related to temperatures, growth rate, or other factors during development. Meristic differences within a species may be related to local productivity (Johnson and Barnett 1975) and possibly the associated growth rate; Mukhacheva (1981), however, noted a range of differences in gill-raker counts, including those between fish from the seamounts and Japan, but failed to show any relationship with local productivity. Because it seems likely that *M. muelleri* is advected to the central North Pacific from Japan, it would be useful to examine genetic differences between populations from these areas to resolve the relationships among the populations or the exact taxonomic status, because species-level differences have been proposed (N. Parin, pers. comm.).

Although we are uncertain of the size of the southern Emperor populations, they may be related to habitat size. If we consider the areas of the seamount slopes and summit at depths above 500 m as an index of available habitat, then the southern Emperor Seamounts have far more extensive habitat than do the small seamounts along the northern Hawaiian Ridge. Southeast Hancock and Northwest Hancock seamounts, for example, have a combined area of less than 34.4 km^2 at depths above 500 m. Comparable values for the southern Emperor Seamounts are as follows: Colahan Seamount, 19.0 km^2; Kammu Seamount, 469.2 km^2; Kinmei Seamount, 26.6 km^2; Yuraku Seamount, 37.5 km^2; Koko Seamount, 3546.3 km^2. The large areas of these seamounts may indicate larger, more stable populations of *M. muelleri*. In addition, the larger size of these seamounts or banks may result in more complex hydrographic regimes that include recirculation and enhanced population retention as contrasted to smaller seamounts (Loder et al. 1988). The chain of seamounts with populations of *M. muelleri* evident in Figure 1 may serve as stepping stones (Wilson and Kaufmann 1987) for replenishment of the small seamount populations. There may be a southerly directed flow along the axis of the seamounts (Darnitsky 1980, Darnitsky et al. 1984) that could result in transport from the southern Emperor Seamounts to the region of Southeast Hancock Seamount. Although our observations were temporally limited, the currents noted from ADCP observations in this study were highly variable, with intermittent periods of southerly flow. The presence of larger fish 10–40 km from the seamount summits (Figure 5) might indicate dispersal of larger fish. Thus, advection of *M. muelleri* from these seamounts, with their larger populations, would be a likely source of recruitment or replenishment of the relatively small Southeast Hancock population.

Recruitment of large numbers of *M. muelleri* to Southeast Hancock Seamount is an annual feature, as shown by abundances evident over a 5-yr period (1984–1988). We propose that the population is maintained by a combination of local recruitment and periodic replenishment from larger, upstream populations, most likely those from the southern Emperor Seamounts. Recruitment to the same seamounts occurs for the pelagic armorhead, *Pseudopentaceros wheeleri* Hardy; this species remains pelagic for ca. 2 yr before recruitment (Boehlert and Sasaki 1988), and densities of armorhead were high enough to sustain fisheries for several years on those seamounts (Sasaki 1986). Some physical characteristic of seamounts may facilitate recruitment; unique features of seamounts in the open ocean include current-topography interactions and anomalies in the earth's gravitational or magnetic field (Keating et al. 1987). Such features, plus the potential for water to remain trapped above seamounts (Shomura

and Barkley 1980, Dower et al. 1992), may maximize the probability of encounter of these pelagic fauna at seamounts.

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