

Abstract.—Pelagic armorhead *Pseudopentaceros wheeleri* are the target of a directed trawl fishery on many of the southern Emperor–northern Hawaiian Ridge seamounts. The population dynamics of armorhead for the period 1970–90 were reconstructed for Southeast Hancock seamount, the southernmost of the seamounts commercially fished, by using commercial catch-and-effort statistics, various biological measurements, and research stock-survey data. The population declined almost continuously from a 1972 high of 5500 metric tons (t) to a 1989 low of 25 t. In addition to the intense fishery, this decline was due partly to the sporadic pattern of armorhead recruitment. Natural mortality rate was estimated as 0.54/year; however, females had a higher mortality rate than males.

Population dynamics of pelagic armorhead *Pseudopentaceros wheeleri* on Southeast Hancock Seamount

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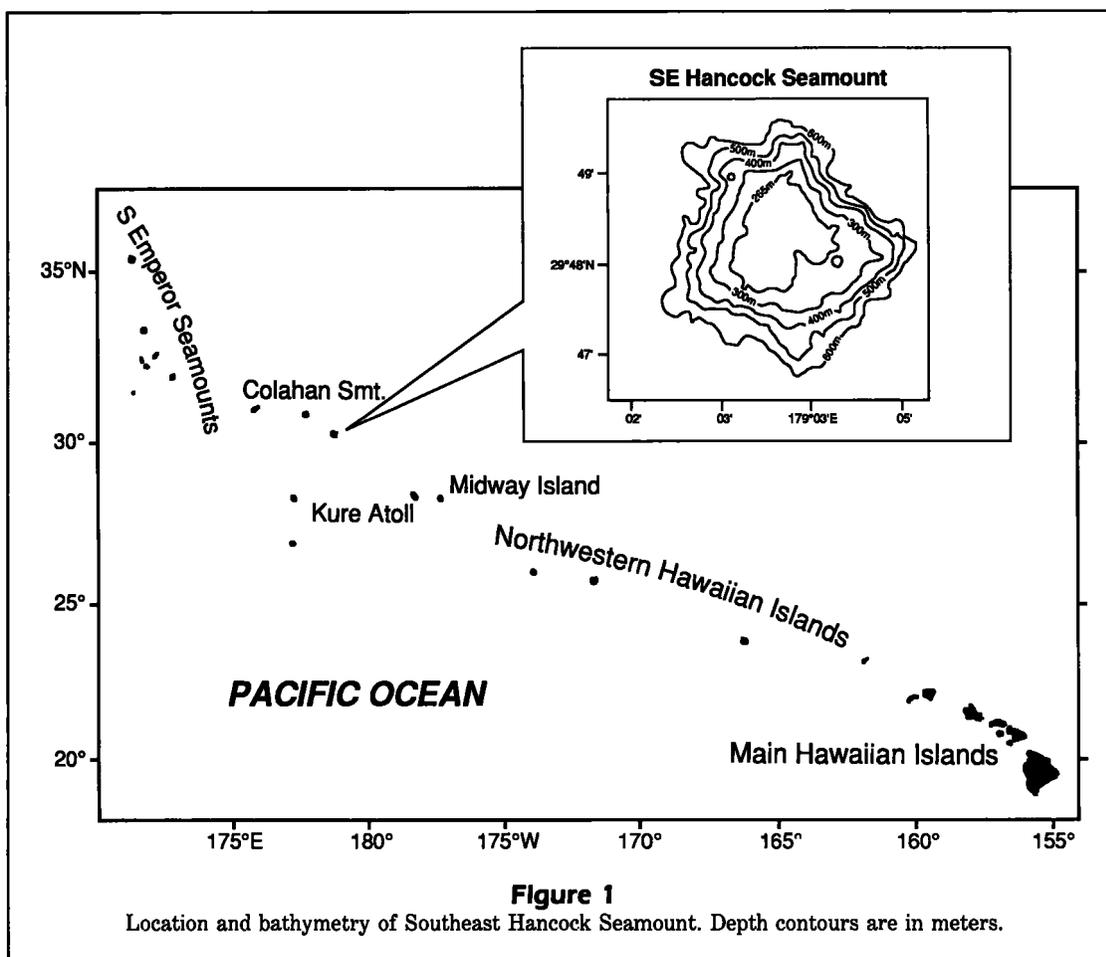
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Pelagic armorhead *Pseudopentaceros wheeleri* have an unusual life history that includes two distinct postlarval phases: a pelagic juvenile phase, and a demersal adult phase. During the first 1.5–2.5 years of their lives (Uchiyama and Sampaga 1990), juvenile armorhead inhabit the epipelagic zone over a broad area of the north-east Pacific, where they acquire large fat reserves before migrating westward to the southern Emperor–northern Hawaiian Ridge (SE–NHR) seamounts (Boehlert and Sasaki 1988, Humphreys et al. 1989). After arriving at the seamounts, armorhead mature and assume demersal habits. Because of the rigors of spawning or the inability to obtain sufficient prey (Seki and Somerton, In prep.), adult armorhead subsequently lose weight to such an extent that they eventually become emaciated and moribund (Humphreys et al. 1989).

Armorhead form dense nighttime aggregations over the relatively flat summits of the SE–NHR seamounts. Soon after these aggregations were discovered in 1967, they were subjected to intense fishing effort first by Soviet trawlers (Komrakov 1970) and 2 years later by Japanese trawlers (Sasaki 1986). The combined annual catch of armorhead rapidly increased and reached a high of

164,000 metric tons (t) in 1973 (Borets 1975, Takahashi and Sasaki 1977) before plummeting to 875 t in 1978. This decline in catch was evidently due to a decline in armorhead abundance, because the Japanese catch-per-unit-effort (CPUE) showed a corresponding drop from a high of 54.0 t/hr in 1972 to 0.4 t/hr in 1978 (Sasaki 1986).

Although never a participant in this fishery, the United States became involved in 1976 when implementation of the Magnuson Fishery Conservation and Management Act extended its exclusive economic zone (EEZ) to include the Hancock Seamounts, the southernmost of the SE–NHR seamounts supporting the armorhead fishery. Although Soviet trawlers ceased operations on the Hancock seamounts after the jurisdictional change, Japanese trawlers continued to fish but were subject to an annual harvest quota and were required to carry U.S. observers who monitored the catch. Regardless of these management efforts, catch rates continued to decline and the Japanese discontinued fishing on the Hancock Seamounts in 1984. In response to the apparent stressed condition of the armorhead population, the National Marine Fisheries Service (NMFS) in 1985 initiated a stock



assessment program to monitor armorhead abundance, and in 1986 enacted a 6-yr moratorium prohibiting trawl fishing on the Hancock Seamounts.

The population dynamics of pelagic armorhead have been previously examined (Borets 1975, Wetherall and Yong 1986); however, the results of these studies are questionable because they were based on either Soviet or Japanese catch-and-effort statistics but not both. The present paper attempts to rectify the problem of incomplete data by focusing solely on the stock of armorhead inhabiting the Southeast (SE) Hancock Seamount, where catch-and-effort statistics were supplemented with various biological and vessel performance data after the initiation of the U.S. observer program in 1977 and were completely replaced by research stock-survey data when the commercial fishery ended. With these additional data, it is possible to obtain absolute estimates of armorhead abundance, rather than relative estimates, and to extend the time-series of such estimates beyond the termination of the commercial fishery. In addition to developing a continuous record of armorhead abundance since the initiation of the

fishery, this paper also includes estimates of the natural mortality rate and annual recruitment of pelagic juveniles to the seamounts.

Materials and methods

SE Hancock Seamount

The Hancock seamounts consist of two peaks, Northwest (NW) and SE Hancock Seamount, separated by 61 km and situated on the NHR ~293 km northwest of Kure Atoll, the northernmost of the Hawaiian Islands, and ~287 km southeast of Colahan Seamount, the closest seamount supporting an armorhead fishery (Fig. 1). The SE Hancock Seamount is shaped somewhat like a truncated cone with a relatively flat, smooth summit and steep, rugged flanks (Fig. 1). This topography, combined with the tendency of armorhead to nocturnally migrate from the flanks to the summit (Humphreys and Tagami 1986), constrained the commercial trawl fishery to operate primarily on the summit (<300 m) at night (Sasaki 1986).

Types of data and preliminary analysis

Since the types of data available for describing the population dynamics of armorhead have changed with time, it is convenient to separate the entire 1970–90 interval into three periods: (1) 1985–90, when NMFS stock surveys were conducted but no commercial fishing occurred; (2) 1978–84, when regulated Japanese fishing occurred with U.S. observers aboard the vessels; and (3) 1970–77, when unregulated Japanese and Soviet fishing occurred.

Period 1 In the period 1985–90, NMFS conducted 10 armorhead stock-survey cruises to SE Hancock Seamount. Although bottom trawls were occasionally used, the primary sampling gear was a bottom longline. Unlike trawls, longlines could be used on the steep flanks of the seamount and allow sampling of the entire population. Longlines consisted of 30 rigid poles (droppers), each with 5 equally-spaced hooks on short leaders, attached at 18m intervals along a 600m groundline (Shiota 1987). On all cruises, longlines were set perpendicular to the depth contours to maximize the depth range sampled and were fished with the same bait (squid), hook size (no. 20 circle), soak time (1 hr), and fishing period (0800–1830 hr) to maintain constant catchability. Starting in 1986, however, catchability changed slightly when hook timers (small timing devices that are activated when a fish strikes the hook; Somerton et al. 1989) were installed on the leaders. To estimate the effect of timers on armorhead catchability, a comparison experiment was conducted in 1990 in which droppers were alternated with and without timers along the longline. A correction coefficient accounting for the effect of timers on catchability was then estimated as the ratio of the armorhead catches for droppers with timers to those without timers (this ratio was 0.77).

Since preliminary information indicated that armorhead density varied with depth on the seamount, stock surveys were based on a depth-stratified sampling design. Fishing depths were estimated by recording a depth profile of the bottom as the longline was set, then partitioning the measured distance between the terminal anchors into 30 equal intervals (the number of droppers). To help correct for possible differences between fathometer depths and actual fishing depths due to horizontal drift while the longline sank, maximum depth recorders were placed on both anchors and at the midpoint of all longline sets. Recorded maximum depths were used instead of fathometer depths to determine where the anchors and midpoint lay along each depth profile.

When longlines were retrieved, the species identity of each captured fish was recorded along with the number of the hook on which it was caught. All fish

from each 5-dropper segment of the longline were then placed together into a basket for later collection of the following biological attributes: sex, fork length (FL, mm), and body depth (BD, mm) which is the shortest distance between the bases of the first anal spine and the dorsal fin. In 1985, body weight (W, g) was also measured on some specimens in addition to body depth. Equations predicting BD from W and FL, and predicting W from BD and FL, were calculated from these data by using multiple regression. These equations are:

Females (*n* 436)

$$BD = 86.69 - 0.19FL + 0.10W \quad (R^2 \ 0.91)$$

$$W = -936.25 + 9.06BD + 2.49FL \quad (R^2 \ 0.90)$$

Males (*n* 476)

$$BD = 75.55 - 0.18FL + 0.10W \quad (R^2 \ 0.85)$$

$$W = -934.02 + 7.52BD + 2.82FL \quad (R^2 \ 0.87)$$

Although the depth distribution of armorhead on the longline could be determined unambiguously with the sampling procedure used, this was not true for the depth distribution of any of the measured or derived biological attributes, because the catch from each 5-dropper segment was aggregated before the attributes were measured. As a means of approximating such depth distributions, the biological attributes of individual fish within each segment group were randomly assigned to the capture depths within the segment.

The relative abundance of armorhead during each stock-assessment cruise was expressed as the mean catch in numbers per hook (\bar{U}) estimated as a weighted average over four depth strata (<265, 265–300, 301–400, 401–500 m). Algebraically, (\bar{U}) is

$$\bar{U} = \frac{\sum_{i=1}^4 U_i A_i}{\sum_{i=1}^4 A_i}, \quad (1)$$

where U_i is the catch per hook, and A_i is the bottom area in depth stratum i . Values of U_i were corrected for the influence of hook timers, and values of A_i were estimated as planar areas between the strata depth boundaries measured on a bathymetric map of the SE Hancock Seamount (Fig. 1).

Since armorhead begin to lose weight after arriving at the seamounts, we examined an index of relative fatness (FI), defined as body depth divided by fork length, as an index of post-recruitment age. Frequency distributions of FI were calculated as weighted averages, where the weighting factors were proportional to the estimated abundance of armorhead in each depth stratum. Algebraically, this is expressed as

$$\bar{N}_{\cdot j} = \frac{\sum_{i=1}^4 N_{ij} A_i U_i}{\sum_{i=1}^4 A_i U_i}, \quad (2)$$

where N_{ij} is the number of fish in FI category j and depth stratum i .

The frequency distributions of FI usually display two or three distinct modes which are similar in appearance to the modes often present in length-frequency distributions of temperate fishes. Since armorhead recruitment to the seamounts is seasonal (Boehlert and Sasaki 1988), these modes were assumed to represent annual cohorts of fish. To estimate the proportion of the population contributed by each cohort (P_k) and the mean and variance of its FI distribution, the FI distributions were separated into their component distributions by fitting a distribution mixture model using a procedure developed for length-frequency data (Macdonald and Pitcher 1979).

Several of the year-class modes in the FI distributions were so distinct that they could be followed through the time-series in an orderly progression from when they were fat (high FI) to when they were lean (low FI). This feature of the FI distributions was used in two ways. First, the rate at which armorhead decrease in fatness was estimated by following the particularly strong year-class recruiting to the seamount in 1986. Mean FI of this cohort (μ_k) on each cruise was regressed against the time (in months), and the time squared, since the cohort was considered fully recruited to the seamount. Linearity of the relationship was determined by the significance of the coefficient of the squared term.

Second, the instantaneous natural mortality rate (M) of armorhead was estimated by following two cohorts, one composed of armorhead recruiting to the seamount in 1986 and the other composed of all armorhead present on the seamount during the first cruise in 1985. Relative abundance of each cohort at each time (t) was first estimated as the product of the catch-per-hook and the proportion of the population within the appropriate cohort on each cruise; that is, $P_{k,t} \bar{U}_t$. Instantaneous natural mortality rate was then estimated by regressing the natural logarithm of relative abundance against the time (in months) since the cohort was considered fully recruited. Analysis of covariance (ANCOVA) was used to test whether the slopes of the regression lines (i.e., the estimated values of M) differed between cohorts. A best estimate of M was computed as the average of the estimates for the two cohorts weighted by the inverses of their variances. Additionally, M was estimated for each sex separately, considering only the 1986 cohort. ANCOVA was again used to test whether

the estimated values of M differed between sexes. These and all subsequent applications of ANCOVA herein will first test a model with one slope and two intercepts against a model with two slopes and two intercepts. If such a test is not significant, then a model with one slope and one intercept is tested against a model with one slope and two intercepts.

Period 2 In the period 1978–84, Japanese trawlers conducted 10 fishing trips to SE Hancock Seamount. For all trips, U.S. observers recorded the weight of armorhead caught and the duration of each trawl-haul. In addition, fork length and body weight were recorded for a random sample of armorhead drawn from each haul.

The biomass of armorhead at the start of each fishing trip was estimated by using the Leslie method (Leslie and Davis 1939) in which the change in CPUE over time is related to the cumulative catch removed. Algebraically, this is expressed as

$$U_d = B_0 q - q K_d, \quad (3)$$

where U_d is the daily average catch (in kg) of armorhead per hour of fishing on day d , K_d is the cumulative catch of armorhead up to the beginning of day d , q is the catchability coefficient, and B_0 is the initial biomass. Two parameters (q , B_0) were estimated by regressing U_d on K_d ; variance of B_0 was estimated using the equation from Polovina (1986). Mean catchability, \bar{q}_j , and its variance were calculated from the per-trip estimates.

Frequency distributions of FI were computed the same as for Period 1, except that body depths were not measured but were estimated from body weights and fork lengths using the regression equation previously described. Since the distributions showed apparent cohort modes similar to those observed during Period 1, the mean and variance of the FI distribution for each cohort and the proportional contribution of the cohort to the population were again estimated with a distribution mixture model. The rate at which FI decreased with time was estimated by regressing the mean FI of the cohort recruiting in 1980 against the time (in months), since the cohort was considered fully recruited.

Period 3 In the period 1970–77, Japanese trawlers fished Hancock Seamounts for at least 1 month in every year; however, data from NW and SE Hancock Seamounts could not be separated. Soviet trawlers also likely fished the Hancock Seamounts over this period, but the available Soviet data (Borets 1975) were aggregated over all seamounts and were not useful for determining the stock dynamics on the Hancock Seamounts.

Relative abundance of armorhead was therefore based solely on Japanese data and was calculated as the reported monthly catch divided by the fishing effort (in hr). Annual mean catch-per-hour (\bar{U}_t) and its variance were calculated from the unweighted monthly means. FI could not be calculated during this period due to insufficient data.

Biomass estimation

Armorhead abundance could be estimated in absolute terms as biomass only in Period 2. In the other periods, abundance was estimable in relative terms as CPUE. To allow estimation of biomass from CPUE in Periods 1 and 3 and to allow the merging of all three periods into one continuous time-series, several parameters were required that could be estimated only with data from Period 2. For this reason, we will start by describing the biomass estimation procedures for Period 2.

Period 2 The initial biomass estimates obtained for Period 2 (i.e., Leslie estimates of initial biomass in each year, $B_{0,t}$) may not include the total biomass of armorhead on the SE Hancock Seamount. Instead, the initial estimates may include only the biomass of the fishable stock or that portion of the stock occurring on the summit at night and therefore vulnerable to trawls. The question of whether $B_{0,t}$ includes the total population was addressed by testing the equality of two different estimators of annual recruitment to the seamount. The first (R_1) was calculated as the difference between the estimated biomass in 1 year minus the expected biomass surviving from the previous year. Assuming that the catch was taken in a brief interval at the start of the year, this relationship can be expressed as

$$R_{1,t+1} = B_{0,t+1} - (B_{0,t} - C_t) e^{-M}, \quad (4)$$

where $B_{0,t}$ and $B_{0,t+1}$ are the biomass estimates in years t and $t+1$, C_t is the catch in year t , and e^{-M} is the annual survival rate. The second (R_2), is calculated as the proportion of the biomass composed of recently recruited fish:

$$R_{2,t+1} = B_{0,t+1} P_{r,t+1}, \quad (5)$$

where $P_{r,t+1}$ is the proportion of the population composed of the cohort recruiting in year $t+1$. If $B_{0,t}$ estimates include the total biomass, then they will be appropriately scaled to C_t , and R_1 will equal R_2 . But if the $B_{0,t}$ estimates are less than the total biomass, then R_1 will be greater than R_2 . Equality was tested using the statistic

$$Z = \frac{R_1 - R_2}{\sqrt{\text{Var}(R_1 - R_2)}}, \quad (6)$$

where Z was assumed to be distributed as a normal random variable. Estimates of $\text{Var}(R_1 - R_2)$ were computed as described in the Appendix.

The fishable proportion of the stock (P_f) was estimated in two stages. First, total biomass of the 1980 cohort was estimated for each year in 1980–84, when the 1980 cohort represented more than 90% of the total population, by using an age-structured analysis (Megrey 1989) applied to a single cohort. Starting with a known or assumed value of biomass at the beginning of 1985, this analysis sequentially predicts biomass in each preceding year by accounting for catch and natural mortality. If the catch occurs over a short period at the start of the year, total biomass of this cohort in each year (B^*_t) can be expressed as

$$\begin{aligned} B^*_{t_0-1} &= B^*_{t_0} e^M + C_{t_0-1} \\ B^*_{t_0-2} &= B^*_{t_0-1} e^M + C_{t_0-2} \\ &= B^*_{t_0} e^{2M} + C_{t_0-1} e^M + C_{t_0-2} \\ &\vdots \\ B^*_{t_0-n} &= B^*_{t_0} e^{nM} + \sum_{i=1}^n C_{t_0-i} e^{(n-i)M}, \end{aligned} \quad (7)$$

where $B^*_{t_0}$ is an estimate of total biomass at the start of the last year (t_0) in the time-series (terminal biomass), and C_{t_0-i} is the catch in year t_0-i . Second, the proportion fished in each year ($P_{f,t}$) was then estimated as $B_{0,t}/B^*_t$, and mean P_f was then estimated as the average of the five annual estimates. This estimate of P_f , however, was not unique because it depended on $B^*_{t_0}$, and $B^*_{t_0}$ was chosen arbitrarily because no independent estimate was available. Therefore, the terminal biomass B^*_{85} (the terminal fishing year was defined as 1985 as a later convenience) was estimated along with P_f . Assuming P_f is a constant, the two parameters were estimated by minimizing the weighted sum of squares of the $P_{f,t}$ with weights equal to the inverse of the variance of each $P_{f,t}$.

Once the estimate of mean P_f had been obtained, corrected estimates of the initial biomass in each year (i.e., corrected Leslie estimates) were estimated as

$$B^*_{0,t} = \frac{B_{0,t}}{P_f}, \quad (8)$$

and the mean annual biomasses were then estimated as

$$B_t^* = \frac{U_t}{q_t P_f}, \quad (9)$$

where U_t and q_t are the mean annual CPUE and catchability. Variance of B_t^* was estimated with methods described in the Appendix.

Period 3 Biomass during Period 3 was estimated from the mean catch-per-hour of Japanese trawlers (U_t) as

$$B_t^* = \frac{U_t}{q_j P_f}, \quad (10)$$

where q_j is the mean catchability of Japanese trawlers estimated for Period 2. Variance of B_t^* was estimated with methods described in the Appendix.

Period 1 Biomass during Period 1 was estimated from longline catch-per-hook (U_t) as

$$B_t^* = \frac{U_t W_t}{q_1}, \quad (11)$$

where W_t is the mean individual weight of armorhead caught during sampling Period t , and q_1 is the catchability of the longlines. Estimation of q_1 required an independent estimate of B_t^* for at least one of the sampling periods, and the estimate chosen was the terminal biomass of the 1980 year-class in 1985. Catchability was thus estimated as

$$q_1 = \frac{U_{85} P_{80} W_{85}}{B_{80,85}^*}, \quad (12)$$

where U_{85} is the catch-per-hook, W_{85} is the mean body weight in 1985, $B_{80,85}^*$ is the terminal biomass of the survivors of the 1980 year-class at the start of 1985, and P_{80} is the proportion of the 1985 population composed of the 1980 year-class survivors. Variances of B_t^* and q_1 were estimated with the methods described in the Appendix.

Spawning and recruitment biomasses

Spawning and recruitment biomasses were estimated for Periods 1 and 2 in which FI information was available. Spawning biomass in each year (S_t) was estimated as:

$$S_{t+1} = \left(B_t^* - \frac{C_t}{2} \right) e^{-\frac{M}{2}} (1 - P_{r,t}), \quad (13)$$

where $P_{r,t}$ is the proportion of B_t^* comprised of newly-recruited fish, and all other terms are as previously defined. This formulation assumes that B_t^* was always estimated on 1 July, the midpoint of both the fishing season and the stock-assessment cruise. Natural mortality between 1 July and 31 December, the assumed peak of spawning (Bilim et al. 1978), was accounted for by the term $e^{-M/2}$, where M is the annual instantaneous natural mortality rate. $P_{r,t}$ was estimated as the proportion of the population (P_k) within the modal group with the largest mean FI, or as zero if no modal group had a mean FI > 0.25. $P_{r,t}$ was included in the estimate of spawning biomass because, based on samples collected on the August 1988 stock-assessment cruise (R. Humphreys, NMFS Honolulu Lab., unpubl. data), female armorhead appear to be nonreproductive during the first spawning season after they recruit to the seamounts. Recruitment biomass was estimated as

$$R_t = \left(B_t^* + \frac{C_t}{2} \right) P_{r,t}. \quad (14)$$

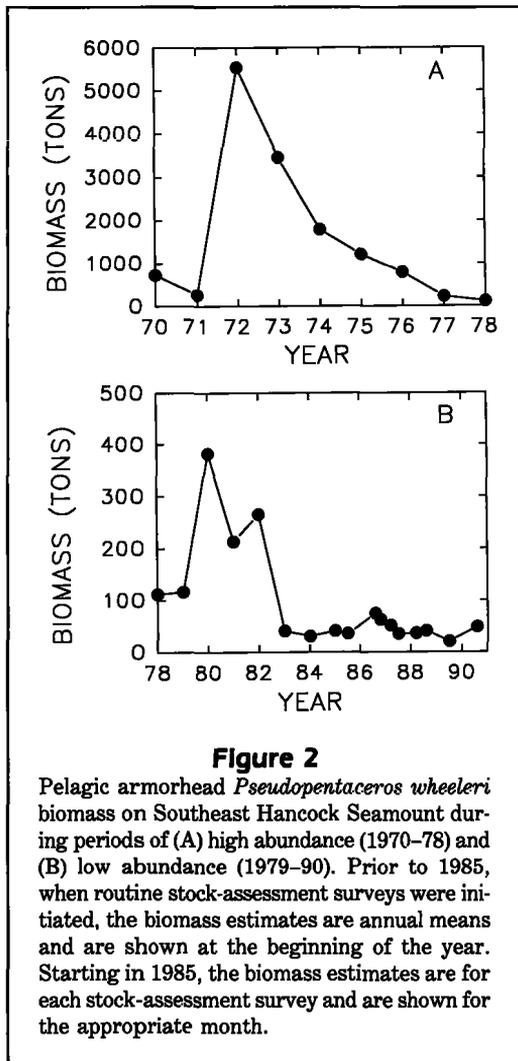
This formulation assumes that recruitment occurs from March to May (Boehlert and Sasaki 1988) and is complete by the time B_t^* is estimated. Since young armorhead recruit to the seamounts at approximately 24–30 months of age (Uchiyama and Sampaga 1990), recruitment follows spawning by 3 calendar years. Spawner-recruit relationships were therefore examined using a 3-year lag between spawning and recruitment.

Results and discussion

The armorhead population on SE Hancock Seamount fluctuated tremendously between 1970 and 1990 (Fig. 2) and declined steadily after the population high in 1972, except for small increases occurring in 1980 and 1986. Before the forces producing these changes (i.e., natural mortality, fishing mortality, and recruitment) are examined, the potential biases and the precision of the biomass time-series will be considered.

Biomass estimates

Construction of the time-series of biomass estimates required (1) merging two time-series of CPUE data that were non-overlapping in time and were from distinctly different gear types, and (2) the conversion of a relative measure of abundance (CPUE) into the absolute measure of biomass. Since Japanese trawls and research longlines were never used simultaneously, the time-series could not be merged by simply standardizing the catchability of one gear relative to the other. Fortunately, however, the armorhead popula-



tion on SE Hancock seamount was sufficiently small and the fishing effort was sufficiently large to allow use of the Leslie method to estimate both the mean catchability of the trawlers (q_j) and the biomass at the initiation of each fishing season ($B_{0,1}$) during the period just prior to replacement of commercial trawling by research longlining. The time-series was merged by using the estimate of q_j and P_f to compute biomass from Japanese trawl CPUE and by using the estimates of $B_{0,t}$ to estimate q_j and thereby compute biomass from longline CPUE. Thus, the Leslie method provided the means to merge the two time-series and to express the resulting time-series in terms of biomass.

Because success of this procedure rests on the successful application of the Leslie

Table 1

Leslie estimates of initial biomass (B_0) and catchability (q) of pelagic armorhead *Pseudopentaceros wheeleri* for each of the Japanese fishing trips during Period 2 (1978–84) on SE Hancock Seamount.

Year	Month	Vessel ID no.	Days fished	Catch (t)	B_0 (t)	q	$P(q=0)$
1978	May	1	11	204	198	0.00197	<0.001
1979	Jun	2	18	68	80	0.00059	<0.005
1980	Aug	3	29	453	551	0.00047	<0.001
1981	Jun	2	5	161	297	0.00101	>0.10
	Aug	3	20	44	55	0.00067	>0.10
1982	May	4	10	180	269	0.00064	0.10
	Jul	2	12	8	17	0.00071	>0.10
1983	Jul	3	19	39	38	0.00066	<0.001

method, any biases in the biomass estimates are likely the result of violations of the underlying assumptions. One of the most important assumptions of the Leslie method is that the change in size of the population is solely due to removals by the fishery. In practice, this requires that the population is closed to immigration and the fishery is sufficiently short and intense so that the effect of natural mortality is negligible. In nearly all cases examined, these requirements were met; that is, fishing usually occurred well after the spring peak in recruitment of pelagic juveniles (Table 1; Boehlert and Sasaki 1988) and the catch was usually obtained in 1 or 2 months and represented a large fraction of the estimated biomass (Table 1). One further indicator of the successful application of the Leslie method is the significance of the slope of the regression, or q . Although the estimates of q obtained using the Leslie method were not always significantly greater than zero, they were remarkably similar among years for each vessel that had fished repeatedly (Table 1). Such similarity was used as justification for using the non-significant estimates in later calculations.

Bias could also result from violation of another assumption of the Leslie method, that the entire population is equally vulnerable to the sampling gear. Such bias was considered likely when initial biomass estimates from Period 2 seemed too small to be consistent with the observed catches. This apparent inconsistency was examined statistically by testing the equality of two estimators of recruitment, one that included catch (R_1 ; Eq. 4), and one that did not (R_2 ; Eq. 5). The bias was confirmed since in 4 of the 5 years examined, R_1 was significantly ($P < 0.05$) greater than R_2 , a condition that could occur only if the biomass estimates were too small.

The most likely explanation for the underestimation of armorhead biomass is that the $B_{0,t}$ estimates do not include the entire population and instead include only the fishable population or the part actually exposed to trawls. This result was surprising because we believed that the population would be sufficiently mixed by the nocturnal vertical migration so that all armorhead would be equally vulnerable even though the trawls were topographically restricted to only a part of the armorhead depth range. Our

finding, however, indicates either that mixing is minimal or that the rate of mixing is relatively low compared with the 2- to 4-week duration of a typical Japanese fishing trip.

Although the bias in $B_{0,t}$ was corrected by estimating the proportion of the stock vulnerable to trawling ($P_f = 0.27$), adequacy of this correction rests on the assumption that P_f does not vary with time. However, P_f may vary with time because the depth distribution of armorhead may vary. For example, the proportion of the population occurring in the shallowest depth stratum (<250 m) averaged 15% over the 10 research cruises, but ranged from 0 to 40%. It is unclear if such variation in the daytime distribution is reflected in the nighttime distribution, because armorhead do not feed at night and therefore cannot be sampled effectively with longlines (M.P. Seki and D.A. Somerton, NMFS Honolulu Lab., unpubl. data). Bias in the biomass estimates could additionally occur if P_f depends on the degree of mixing of deep and shallow fish, because P_f would likely be larger when fishing periods were longer and less intense. Since fishing periods tended to be longer during Period 3 than in Period 2, this would lead to an overestimate of biomass during Period 3.

Precision in the estimates of biomass, which is expressed as the coefficient of variation (CV) to compensate for the large range in biomass, was smallest in Period 1 (Fig. 3), because longline CPUE estimates were more precise than trawl CPUE estimates. Expressed differently, based on the mean CV over the period 1970–84 (excluding 1971 when data were not sufficient to estimate the variance of U_t), the 95% confidence intervals for B^*_T was $\pm 1.70 B^*_T$, which in all years includes zero. Over the period 1985–90, however, the 95% confidence interval was $\pm 0.29 B^*_T$, and never included zero.

Post-recruitment ageing

The estimates of natural mortality rate and annual recruitment required estimates of the age distribution. Although the ages of armorhead can be determined using either daily or annual growth increments on their otoliths (Uchiyama and Sampaga 1990), they are easily obtainable only for individuals in the pelagic phase of their life history, because somatic growth ceases once armorhead recruit to the seamount (Humphreys et al. 1989) and growth increments become so closely spaced that they are exceedingly difficult to count (R. Humphreys, NMFS Honolulu Lab., pers. commun.). Thus, we expressed age on a scale relative to the presumed time of recruitment. Such post-recruitment ages were based on the decrease in FI over time.

Frequency histograms of FI display modes which can be tracked sequentially from one histogram to the next over time as they move from the right (high FI or fat) to the left (low FI or lean). Two examples of this are the

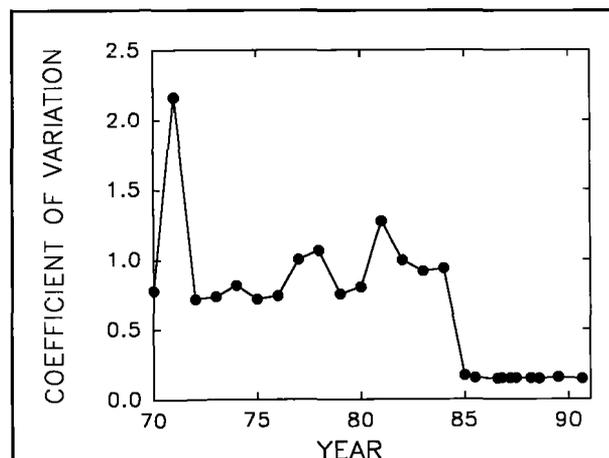


Figure 3

Coefficient of variation of the biomass estimates of pelagic armorhead *Pseudopentaceros wheeleri* as a function of time.

large mode that appeared in 1980 and could be followed until 1984 (Fig. 4A) and the large mode that appeared in 1986 and could be followed until 1990 (Fig. 4B). Since the first appearance of these modes was always associated with an increase in CPUE (Fig. 2B), they were interpreted to represent cohorts of fish that had recruited to the seamount.

To further substantiate our interpretation of the modes, the rate of decrease in FI was examined for consistency both over time and between the two presumed year-classes. Plots of FI versus time appeared to have slight curvature (Fig. 5), but for both the 1980 and 1986 year-classes the curvature was not significant ($P > 0.05$). Changes in FI, therefore, are proportional to changes in post-recruitment age. The rates of decrease in FI of the 1986 (0.00169/mo) and the 1980 (0.00157/mo) year-classes did not differ significantly (ANCOVA, $P > 0.05$). In addition, sexual equality in the rate of decrease in FI was tested for the 1986 year-class alone, and the male rate was not significantly different (ANCOVA, $P > 0.05$) from the female rate. Taken together, these findings indicate that all armorhead decrease in FI at approximately the same rate and that once established by the recruitment of a strong year-class, the coherency of an FI mode should be preserved over time.

Natural mortality

Natural mortality was estimated from the change in the relative abundance of two cohorts over time during a period when no commercial fishing occurred. The first of these cohorts, which consisted

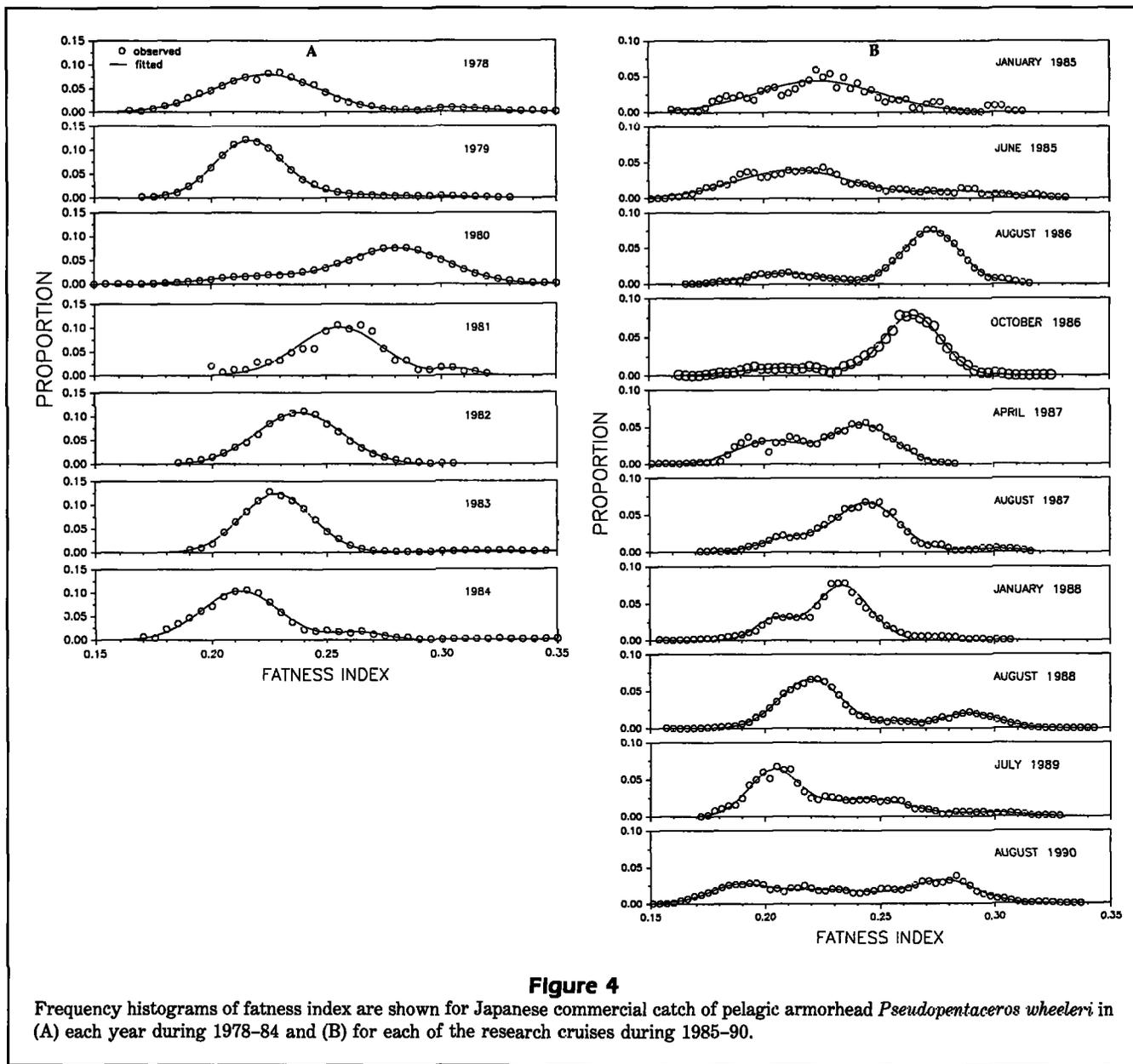


Figure 4

Frequency histograms of fatness index are shown for Japanese commercial catch of pelagic armorhead *Pseudopentaceros wheeleri* in (A) each year during 1978-84 and (B) for each of the research cruises during 1985-90.

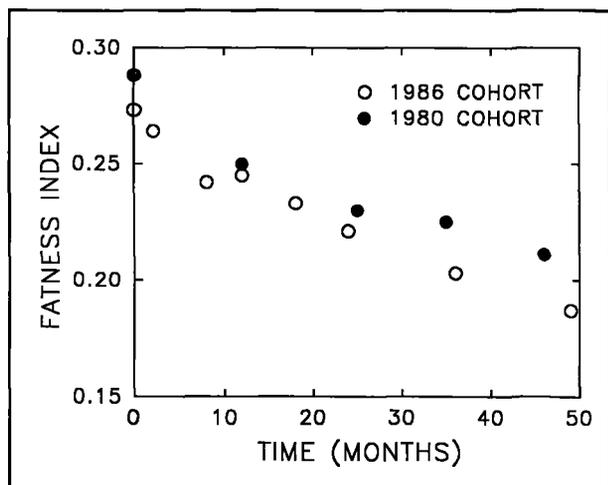


Figure 5

Decrease in fatness index of pelagic armorhead *Pseudopentaceros wheeleri* with time for the 1980 and 1986 year-classes on Southeast Hancock Seamount.

of the extant armorhead population in January 1985, was identifiable for seven consecutive samplings and had an instantaneous natural mortality (M) of 0.054/mo. The second, which consisted of the year-class recruiting in 1986, was identifiable for eight consecutive samplings and had an M of 0.044/mo (Fig. 6). Although the two estimates were significantly different (ANCOVA, $P < 0.05$), the weighted average (0.045/mo or 0.54/yr) was chosen as

the most representative value. For both cohorts, log-relative abundance was clearly a linear function of time, and M is therefore invariant with age (Fig. 6A).

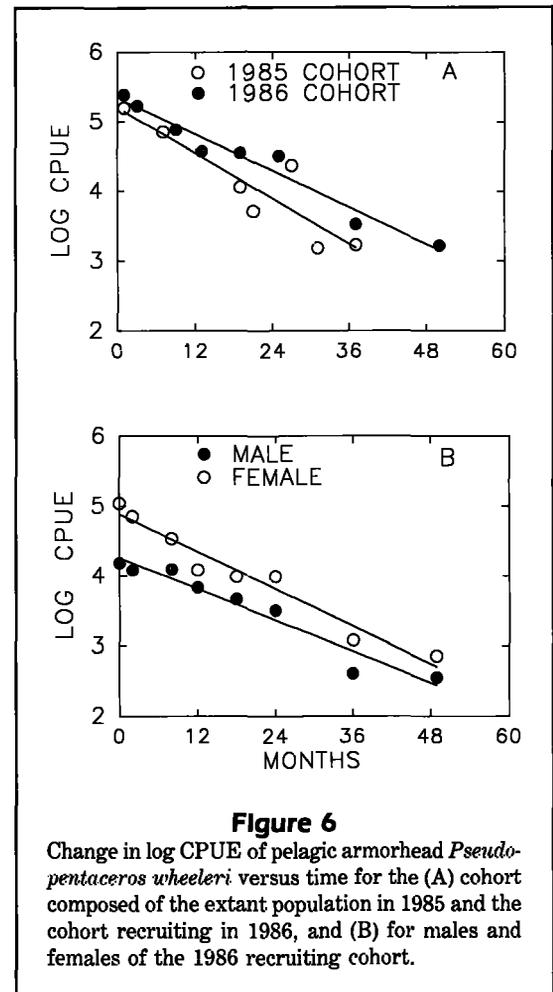
When M was estimated separately for each sex, considering the 1986 cohort alone, the value for males (0.037/mo) was significantly different (ANCOVA, $P < 0.001$) from the value for females (0.045/mo). Furthermore, the intercept of the regression, i.e., the log-relative abundance at the time of recruitment) appeared to be smaller for males (4.27) than for females (4.94), but the difference could not be tested because of the strong difference in slopes (Fig. 6B). Taken together, these results indicate that, at least for the 1986 cohort, females recruited to the seamounts in greater abundance than males but subsequently died at a greater rate. It is also possible that the higher mortality rate of females was primarily restricted to the first year of residence on the seamount (Fig. 6B).

Since a sexual difference in mortality seemed inexplicable to us, we examined the possibility that longlines preferentially selected fat females. This was done by examining whether the ratio of females to males, expressed as proportion female, changed with FI similarly for trawls as for longlines. Since the FI values of females and males decrease identically with time, any change in female proportion with FI would indicate either selective sampling or differential mortality, depending on whether one or both gear types showed the change. To test for such changes, female proportion was regressed on FI for various samples. When these regressions were performed on the longline samples, all 10 had a significant ($P < 0.05$) positive slope. When the regressions were performed on the research trawl samples, four of five had a significant positive slope. Thus a sampling bias is unlikely, unless both gears produced a similar bias.

The estimate of natural mortality rate (0.54/yr) is more than twice that reported in Borets (0.25/yr; 1975). His estimate, however, was based on age data that were likely biased for two reasons. First, the age range [i.e., 7 yr, ages 5–12], reported in Borets (1975) appears to be excessive when compared with the range estimated from modal progression through the research FI histograms (4–5 yr). Second, the mean age of the catch between 1968 and 1974 reported in Borets (1975) did not decrease as would be expected in a developing fishery. On the other hand, our estimate of natural mortality rate was less than the rate implied in the studies of Uchida and Tagami (1984), Humphreys et al. (1989), and Uchiyama and Sampaga (1990), which all suggested that armorhead were semelparous and, like Pacific salmon *Oncorhynchus* spp., died soon after spawning.

Fishing mortality

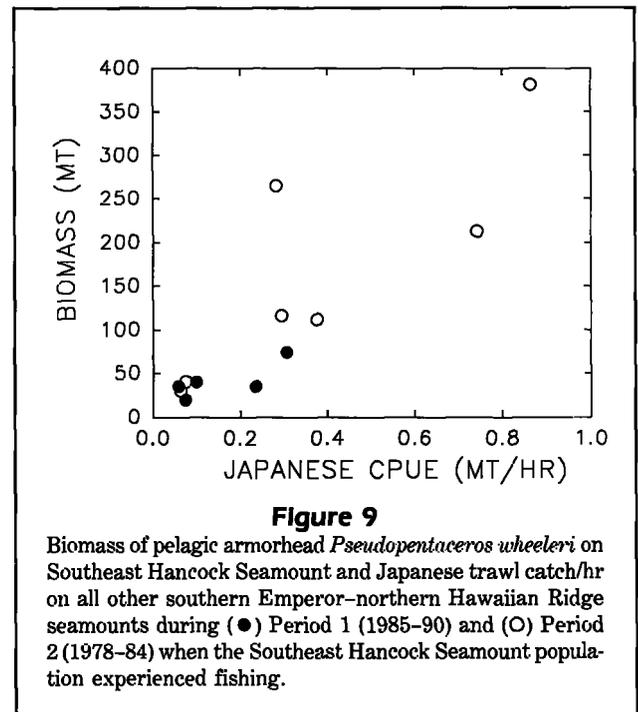
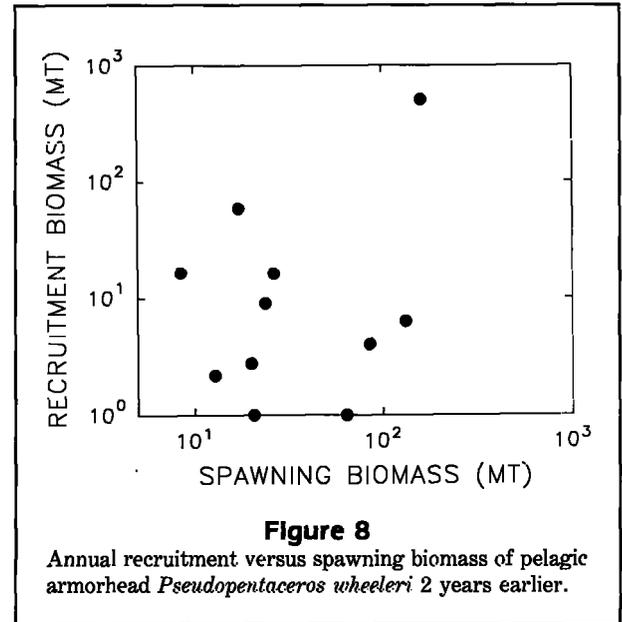
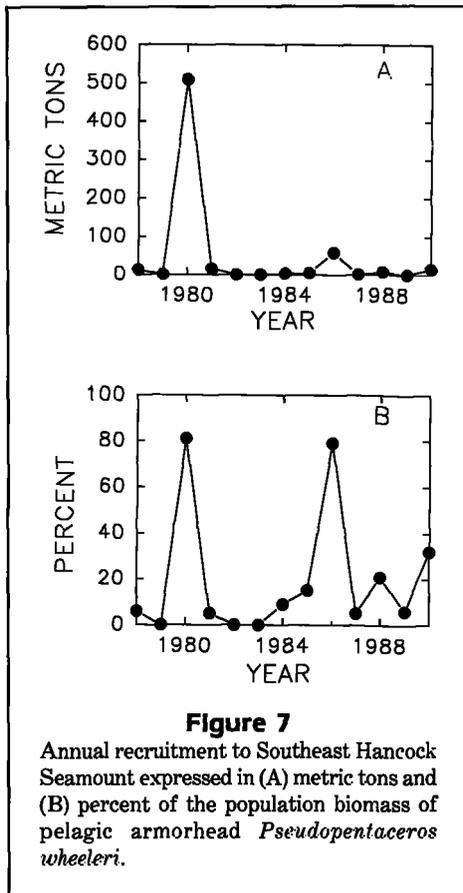
Fishing mortality rate (F) can be estimated only between 1978 and 1983 when the total catch and effort on SE Hancock Seamount are known with reasonable certainty, based on the U.S. observer program. Over this period, F , which was calculated as the estimated value of $q_j \times$ total annual effort, averaged 1.03/yr or roughly twice the natural mortality rate. The mean



exploitation rate (which was approximated as $(F/Z) (1 - e^{-Z})$ where $Z = F + M$), was ~ 0.50 . Therefore, provided that no recruitment occurred and that fishing effort was continuous throughout the year, then an average of roughly 50% of the population at SE Hancock Seamount was removed annually by the fishery over this period.

Recruitment

Annual recruitment to SE Hancock Seamount was extremely intermittent between 1978 and 1990. When expressed in metric tons, the 1980 recruitment clearly dominated the entire record (Fig. 7A). However, the total biomass changed considerably over this period, and, when expressed as a percentage of the total biomass, the 1986 recruitment and—to a lesser extent—the 1988 and 1990 recruitments were also relatively important (Fig. 7B). For some



unknown reason, recruitment in the even years tended to be larger than it was in the odd years (Mann-Whitney test, $P = 0.06$).

Prior to 1978, it is difficult to estimate annual recruitment because the data required to calculate FI were not routinely collected. However, an examination of the large increase in abundance in 1972 (Fig. 2A) cannot be avoided. Interpretation of the 1972 increase is troublesome because the evidence for an unusually large recruitment is equivocal. A large recruitment, for example, should have resulted in a large increase in the proportion of the population comprised of fat armorhead as it did in 1980 and 1986 (Fig. 4A, B), yet the proportion of the population categorized as fat during the period of maximum recruitment was smaller in 1972 than it was in 1973 when recruitment did not appear to be exceptionally large (Boehlert and Sasaki 1988). Armorhead measured in 1972, however, were markedly smaller than in any other year (Takahashi and Sasaki 1977, Borets 1975). One proposed explanation for the small size is that the tremendous abundance of armorhead in 1972 resulted in a density-dependent suppression of growth in the pelagic phase (Borets 1977). This might also have reduced the FI of recruits

and thereby masked the FI signature of a large recruitment.

An alternate explanation for the 1972 increase in abundance is that it is an illusion due to a rapid increase in trawl catchability as the newly-developed fishery progressed from an exploratory phase to a production phase (Takahashi and Sasaki 1977, Uchida and Tagami 1984). If, however, the 1972 increase was due simply

to changing catchability, then such an increase should not be evident in the Soviet catch-and-effort data, because the Soviet fishery had developed earlier and was likely beyond its "fishing-up" phase. Soviet data do display an increase from 1971 to 1972 (73–104 million fish/vessel day; Borets 1975), but this is considerably less than that experienced by the Japanese fishery. Thus, it is not entirely clear whether the apparent increase in 1972 was real and due to recruitment or an artifact due to changing catchability.

The dependance of recruitment on spawning biomass was examined by Wetherall and Yong (1986) and found to be essentially nonexistent, at least at the high levels of spawning biomass extant during 1969–77. Recruitment, however, must ultimately be limited by spawning biomass at low population levels; therefore, we reexamined the relationship over the period 1980–90, when the spawning biomass was considerably lower. This was done by plotting, on a log-log scale, the estimated spawning biomass on SE Hancock Seamount against the estimated recruitment 2 years later (Fig. 8). Since a clear relationship is not evident, it is possible that recruitment and spawning biomass are only weakly related even at the low population levels examined. There are, however, at least two other possible reasons why no relationship was found. First, since no apparent genetic difference exists among the armorhead collected at the various seamounts (Borets 1979), recruits to SE Hancock Seamount are likely the progeny of the entire North Pacific population. If the SE Hancock Seamount population does not vary concordantly with the entire North Pacific population, any relationship between recruitment and spawning biomass would be obscured. However, plots of the estimated biomass on SE Hancock Seamount against Japanese CPUE on all SE–NHR seamounts show a strong concordance (Fig. 9). Second, if spawning biomass does exert an influence on recruitment, it may do so only by limiting the maximum level attained. Thus, at higher levels of spawning biomass, higher levels of recruitment are possible—but not assured—because of environmental variability. One interpretation of Figure 8 could therefore be that recruitment did increase with spawning biomass, but at the higher levels of biomass there were several environmentally-poor recruitment years.

Management implications

Since armorhead do not grow after they recruit to the fishery and therefore cannot be growth-overfished, management strategies could be designed solely to achieve some optimum level of spawning stock biomass (SSB). One approach is to define this optimum SSB by

using a spawner-recruit relationship as is done for some species of Pacific salmon (Ricker 1975). Another approach is to define it in terms of a fixed percentage of the equilibrium biomass in the absence of a fishery (Beddington and Cooke 1983). But in either case, the spawning population must include the entire SE–NHR population rather than the small component examined here. In addition, some form of international agreement controlling the armorhead catch will be required before any management measures are effective.

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Appendix

Variances of several of the estimators described in Materials and Methods were approximated by using the Delta method (Seber 1973) and assuming all covariance terms were negligible. Variance of $(R_1 - R_2)$ was estimated as

$$\text{Var}(R_1 - R_2) = (P_{r,t+1} - 1)^2 \text{Var}(B_{0,t+1}) + (B_{0,t+1})^2 \text{Var}(P_{r,t+1}) + e^{-2M} [\text{Var}(B_{0,t}) + \text{Var}(C_t) + (B_{0,t} - C_t)^2 \text{Var}(M)], \quad (15)$$

where all variables are defined in text Equations 5 and 6. Variances of $B_{0,t}$ and $B_{0,t+1}$ were computed by using the method in Polovina (1986). Variance of C_t was assumed to be negligible because catch was measured by U.S. observers. Variance of M was estimated as the variance of the slope of the regression of log-relative abundance on postrecruitment age (in years). Variance of $P_{r,t+1}$ was estimated with a bootstrap method (Efron and Gong 1983). Bootstrap estimates were obtained from trawl samples of armorhead biological data by iteratively repeating the following steps: (1) A subsample of n fish from each sample was randomly chosen with replacement, where n is equal to the size of the original sample; (2) an FI frequency distribution was constructed from the subsample; (3) $P_{r,t+1}$ was estimated by fitting the distribution mixture model to the FI frequency distributions. In all cases, variance of $P_{r,t+1}$ was calculated as the variance among 100 bootstrap estimates.

Variance of B_t^* during Period 2 was as

$$\text{Var}(B_t^*) = \left[\frac{1}{q_t P_f} \right]^2 \text{Var}(U_t) + \left[\frac{U_t P_f}{(q_t P_f)^2} \right]^2 \text{Var}(q_t) + \left[\frac{U_t q_t}{(q_t P_f)^2} \right]^2 \text{Var}(P_f) \quad (16)$$

where all variables are defined in Equation (9). Variance of U_t was estimated as the variance among the daily U within each year. Variance of q_t was estimated as the variance of the slope of the Leslie model. When more than one vessel fished in each year, however, variance of q_t was the average of the individual variance estimates weighted by catch.

Variance of P_f was estimated by using a Monte Carlo model. Each iteration of the model consisted of generating a random value of $B_{0,t}$ for each year and a value of M , assuming all were normally distributed with means and variances equal to the original estimated values. With these generated values, B_t^* was estimated for each year with Equation (9) and $P_{f,t}$ was estimated as $B_{0,t}/B_t^*$. Mean estimates of P_f and $B_{80,85}^*$ (B_{t0}^* in Eq. 7), were obtained by using the iterative procedure to minimize the weighted sum of squares of the $P_{f,t}$ estimates. In all cases variances of P_f and $B_{80,85}^*$ were estimated from 100 iterations of the Monte Carlo model.

Variance of B_t^* during Period 3 was estimated using Equation (16) but with q_t replaced by q_j . Variance of U_t was estimated as the variance among the monthly means. Variance of q_j was estimated as the variance among the q estimates in Table 1. Variance of P_f is the same as for Period 2.

Variance of B_t^* during Period 1 was estimated as

$$\text{Var}(B_t^*) = \left[\frac{W_t}{q_1} \right]^2 \text{Var}(U_t) + \left[\frac{U_t}{q_1} \right]^2 \text{Var}(W_t) + \left[\frac{U_t W_t}{q_1^2} \right]^2 \text{Var}(q_1), \quad (17)$$

where all variables are defined in Equation (11). Variance of W_t was estimated from the biological samples from each research cruise. Variance of U_t was estimated as the variance of U among the four depth strata.

Variance of q_1 was estimated as

$$\text{Var}(q_1) = \left[\frac{U_{85} W_{85}}{B_{80,85}^*} \right]^2 \text{Var}(P_{80}) + \left[\frac{U_{85} P_{80}}{B_{80,85}^*} \right]^2 \text{Var}(W_{85}) + \left[\frac{P_{80} W_{85}}{B_{80,85}^*} \right]^2 \text{Var}(U_{85}) + \left[\frac{U_{85} P_{80} W_{85}}{B_{80,85}^*} \right]^2 \text{Var}(B_{80,85}^*), \quad (18)$$

where all variables are defined in Equation (12). Variances of W_{85} and U_{85} were estimated as described above for W_t and U_t . Variance of P_{80} was estimated as described for $P_{r,t+1}$. Variance of $B_{80,85}^*$ was estimated with the previously described Monte Carlo model.