

POPULATION BIOLOGY OF RED ABALONES, *HALIOTIS RUFESCENS*, IN SOUTHERN CALIFORNIA AND MANAGEMENT OF THE RED AND PINK, *H. CORRUGATA*, ABALONE FISHERIES

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ABSTRACT

Population dynamics of red abalones, *Haliotis rufescens* Swainson, were studied at Johnsons Lee, Santa Rosa Island, California from 1978 through 1982 and in 1984. Tagging studies were used to calculate the von Bertalanffy growth parameters. Size-frequency distributions were used to assess settlement rate and fishable stock, and to estimate the natural mortality rate. These results were employed in yield-per-recruit and egg-per-recruit analyses; similar calculations were made for pink abalones, *H. corrugata* Gray, using values from the literature. Our analyses suggest that present sport and commercial minimum legal sizes allow for adequate egg production to maintain stock sizes; simple recruitment overfishing is not a satisfactory explanation for the sharp and continuing decline in landings of both species. We consider other factors which may be responsible and argue that prudent abalone management should maintain egg-per-recruit at the cost of some potential yield.

The red abalone, *Haliotis rufescens* Swainson, is the largest member of its genus and historically the most important species in the California abalone fishery. Ranging from Coos Bay, OR to Bahia Tortugas, Baja California (Cox 1962), red abalones are found along the entire coast of California but almost all of the commercial harvest comes from Point Conception south (Fig. 1). The recovery of the sea otter, *Enhydra lutris*, population has precluded the commercial fishery within its central California range (Miller and Geibel 1973; Hardy et al. 1982; Estes and Van Blaricom 1985) and the north coast has been reserved for the recreational fishery since 1945 (Cicin-Sain et al. 1977). Today the major commercial red abalone fishing grounds are in southern California—the northern Channel Islands, Santa Cruz, San Miguel, San Nicolas, and Santa Rosa Islands—and mainland sites where upwelling produces cooler temperatures which are north and west of Santa Barbara and near San Diego. Red abalones are also found on the Palos Verdes Peninsula within the coastal area closed to all abalone fishing. The present size limits are 178 mm for the recreational fishery and 197 mm for commercial harvest.

The pink abalone, *H. corrugata* Gray, is found from Point Conception, CA (Cox 1962) to Punta Abreojos, Baja California (Doi et al. 1977). From 1949 to 1970, pink abalones supported a fishery

equal in importance to the red abalone fishery. In 1970, an increase in the minimum legal commercial size from 152 to 159 mm caused a sharp decrease in landings (Tegner 1989). The present size limits are 152 mm for sport and 159 mm for commercial harvesters.

Despite the high landed value and the recreational importance of the abalone fishery in California, no stock assessments are available. Management has been based on the assumption that an appropriate size limit will protect the stocks. An appropriate size limit is considered to be one large enough to allow sublegal abalones to spawn several times before being recruited to the fishery, yet small enough that the size is attained within a reasonable number of years after settlement (Burge et al. 1975). A strong dependence on a minimum size limit is consistent with abalone fishery management elsewhere. In his review of world abalone fisheries, Harrison (1986, p. 21) suggested that "an appropriate set of effectively policed minimum size regulations is the cornerstone of managing these fisheries." Despite the importance of the size limit in managing California abalone fisheries, no analysis of its effect on population dynamics or fisheries yield has been published.

After many years of relative stability, the red and pink abalone harvests began a marked decline in the late 1960s (Burge et al. 1975; Cicin-Sain et al. 1977). Despite limitation of entry to the commercial fishery and tighter restrictions on the recreational fishery in the mid-1970s, the decline in landings has con-

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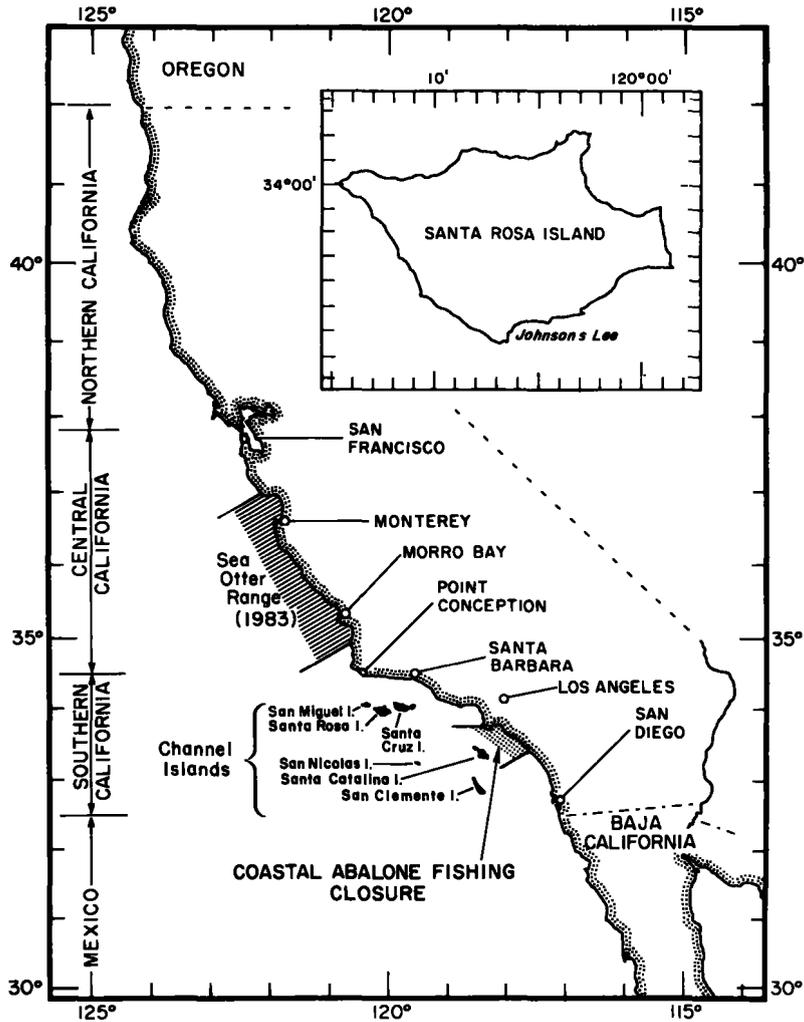


FIGURE 1.—Map of California illustrating the study site and other locations described in the text.

tinued into the late 1980s (Tegner 1989). Several possible causes of the decline have been identified (Burge et al. 1975; Cicin-Sain et al. 1977; Tegner 1989) including sea otter predation in central California, mortality caused by removing and replacing sublegal abalones, environmental changes, inappropriate size limits, and failure of larval recruitment. The last is frequently invoked as a problem in abalone fisheries (e.g., Harrison 1986). Furthermore, because of the central California origin of the red abalone fishery (Cox 1962), little is known about the life history of this species in southern California. Warmer temperatures, different current patterns, and changes in food availability relative to central

California are likely to affect population parameters important to the management of the fishery.

To provide a better basis for management of the fishery and for the evaluation of seeding experiments, the University of California Sea Grant College Program and the California Department of Fish and Game (CDFG) conducted a joint study of red abalones at Johnsons Lee on Santa Rosa Island. The site was visited annually during the second week of July from 1978 through 1982 and in June 1984. During the first four visits, 2,145 animals were tagged for growth studies (Haaker et al. 1986); these data were used to calculate the von Bertalanffy growth parameters (Haaker et al. in prep.).

Here we report the results of five years of population studies conducted concurrently with the tagging studies. The objectives were to assess the rates of settlement of young-of-the-year abalones and to follow changes in size-frequency distributions and densities of animals above and below the recreational and commercial fishery minimum size limits. Predator densities and empty shells were used to study predation patterns.

We then use results of the joint study to evaluate the appropriateness of the present size limit for red abalones in southern California. Yield-per-recruit analyses have been commonly used to evaluate size limits and levels of fishing mortality for abalones (e.g., Isibasi and Kojima 1979; Harrison 1983, 1986; Sluczanowski 1984, 1986; Clavier and Richard 1985; Breen 1986). Sluczanowski (1984, 1986), however, showed that egg production from a cohort of females could be reduced to a very small fraction of egg production from an unfished cohort at size limits and fishing rates that seemed reasonable in yield-per-recruit analyses. He suggested that size limits and fishing rates should be examined in the light of both yield- and egg-per-recruit analyses. This approach was used by Breen (1986) for northern abalones, *H. kamtschatkana*, in British Columbia. Egg-per-recruit analyses have also been used widely in assessing size limits for the American lobster, *Homarus americanus*, fishery (Saila and Flowers 1966; Campbell 1985; Ennis 1985).

In this study, we use growth estimates and size-frequency distributions to estimate the natural mortality rate of red abalones, using the method of Fournier and Breen (1983). The mortality and growth estimates are then employed in a yield-per-recruit analysis, using the method of Beverton and Holt (Ricker 1975); and with fecundity data in an egg-per-recruit analysis described below. Results of the egg- and yield-per-recruit analyses are examined together, and implications for management of the red abalone fishery are described. A similar analysis is carried out for pink abalones using data from Tutschulte (1976) and Doi et al. (1977) to consider the generality of the results.

MATERIALS AND METHODS

Field Studies

Johnsons Lee is located on the south coast of Santa Rosa Island (lat. 33°54'N, long. 120°06'W). It is protected from the prevailing northwesterly wind and swell typical of summer but is open to the south and east. In part because of this protection,

Johnsons Lee is frequented by both sport and commercial fishermen. The *Macrocystis pyrifera* canopy was generally about a kilometer wide by two or more kilometers in length during this study. The substrate consisted of rocky reefs separated by a network of sand channels. The vertical relief was quite variable but ledges, crevices, and rock piles provided extensive abalone habitat. *Macrocystis* and several species of foliose reds were the most abundant algae; other common plants included *Pterygophora californica*, *Egregia menziesii*, *Laminaria farlowii*, *L. setchellii*, *Desmarestia* spp., *Cystoseira*, spp., articulated and encrusting coralline algae, *Codium fragile*, *Ulva* sp., *Phyllospadix* sp., and *Zostera marina*. Drift algae were abundant.

The 300 × 1,200 m study site was located with its long axis parallel to shore and divided in half by a line perpendicular to shore; the goal was to divide effort evenly between the two areas. The transect protocol was adapted from a previous CDFG study of red abalones at Point Estero (Ebert et al. in prep.) so that the results would be directly comparable. Sampling strategy was based on the method of simple random sampling. Randomly selected transect origins were located with the use of buoys marking corners of the study areas and compass headings to terrestrial topographic features. Transects were tied to the skiff anchor and laid on a 60° compass course paralleling the shoreline and depth contours. Transect depths varied from 7 to 16 m. Bat rays, *Myliobatis californica*, and California sheephead, *Semicossyphus pulcher*, were counted as the line was laid and horizontal visibility was estimated to calculate the density of these predators. The 30 m transects were divided into eight quadrats, each 7.5 × 2 m. Habitat was graded as sand (<25% rock), rock/sand (<75% rock), and rock (>75% rock). Transects that fell on habitat which was greater than 50% sand were not sampled; alternate locations had been pre-selected. Benthic predators were counted, all abalones visible without disrupting the substrate or the use of an underwater light ("emergent" abalones) were measured, and algae and sea urchins were noted by species and graded as sparse, common, or abundant in each quadrat. Two randomly selected quadrats were destructively sampled. Red (*Strongylocentrotus franciscanus*) and purple (*S. purpuratus*) sea urchins and kelps were counted, all urchins were moved to expose juvenile abalones under their spine canopies, and all rocks turned to locate non-emergent abalones. All abalone shells were collected for measurement and description of shell damage. Transect sample sizes were limited by manpower in 1978 and winds in 1979. To augment shell sample

sizes, all shells encountered in the tagging area (contained within the study site) were measured from 1980 on. Because of the low number of abalones recovered in the random quadrats in 1981, additional quadrats were selected to increase the sample size for the mortality analysis. A sixth visit was conducted in June 1984 to assess the effects of the strong El Niño of 1982–84 (Tegner and Dayton 1987) on the growth of the tagged abalones; shells were also collected at this time.

Mortality Rate

Total mortality rate was estimated from the length-frequency data using the method of Fournier and Breen (1983; Breen and Fournier 1984). For each year, observed numbers in each 3 mm length interval were converted to proportions of the total sample, then multiplied by the density in the destruct quadrats. Observations were then summed for all years 1978–82, and then multiplied by 100 as numbers were so small. The Fournier and Breen

method simultaneously estimates the mean lengths-at-age, the standard deviations of lengths-at-age around their mean, the variance of mean lengths around a von Bertalanffy growth curve, the three von Bertalanffy growth parameters (t_0 , asymptotic length L_∞ , and Brody coefficient K), total instantaneous mortality rate Z , the population proportions-at-age, and the variance of proportions-at-age around a smooth exponential decay curve. Some of these estimates can be fixed or constrained so that existing knowledge is used in obtaining estimates. The number of age classes and various initial conditions must be specified.

Fournier and Breen (1983) used this method to estimate natural mortality rate by sampling abalones in unfished populations. In the population described here, we can estimate only total mortality rate because the population has been subjected to exploitation. The natural mortality rate must be less than this estimate. The minimum legal size for the commercial fishery is close to the average maximum size, and because this method estimates average

TABLE 1.—Parameter values and initial conditions used in estimating mortality rates of red abalones, and their rationale. Parameters without good rationale were varied (see Table 6) to determine the sensitivity of the estimate.

Parameter	Value	Rationale
Number of age classes, NK	Varied, 12–16	Growth curve; 16 is the maximum number handled by the program
Age of first fully sampled cohort, $NFULL$	Varied, 1–4	Growth curve, sampling considerations
Lower bound on K	0.269	Tagging results (Haaker text fn. 3)
Permitted variance of means around von Bertalanffy curve and population proportions around smooth curve	1.0	No reason to force any other result
Lower bound on the first SD	Varied, 7.5, 1.0	Inspection of Figure 3
Upper bound on the first SD	Varied, 8.5, 10.5, 15.5	Inspection of Figure 3
Lower bound on the last SD	Varied, 7.5, 1.0	Inspection of Figure 3
Upper bound on the last SD	Varied, 8.5, 10.5, 15.5	Inspection of Figure 3
Bounds on population proportions	0.0, 1.0	No constraints used
Bounds on mean lengths-at-age	0–300, ages 2 to $NK-1$	Last mean constrained to force estimate of L_∞ of 201 mm per tagging results (Haaker text fn. 3)
Initial conditions		
K	0.271	Based on tagging results
First mean length	30 mm	Based on tagging results, inspection of Figure 3
Last mean length	199 mm at age 16, adjusted slightly for choice of NK	Based on tagging results
First SD	8.0	Inspection of Figure 3
Last SD	8.1	Inspection of Figure 3

total mortality rate over most of the size and age range, we believe that the method gives an estimate of the total mortality rate which is not much greater than the natural mortality rate.

Initial values and bounds, and their rationales, are shown in Table 1. We forced the estimation procedure to produce estimates of growth rate parameters consistent with the tagging results from Johnsons Lee (P. Haaker³). The lower bound on K

was set at 0.269, resulting in an estimated K equal to this; and the last mean length was constrained so as to obtain an estimated L_{∞} of 201 mm. Bounds on the standard deviations of lengths-at-age around their means were based on inspection of the length-frequency data (Figs. 2, 3).

³P. L. Haaker, California Department of Fish and Game, 330 Golden Shore, Long Beach, CA 90802, pers. commun. 1986.

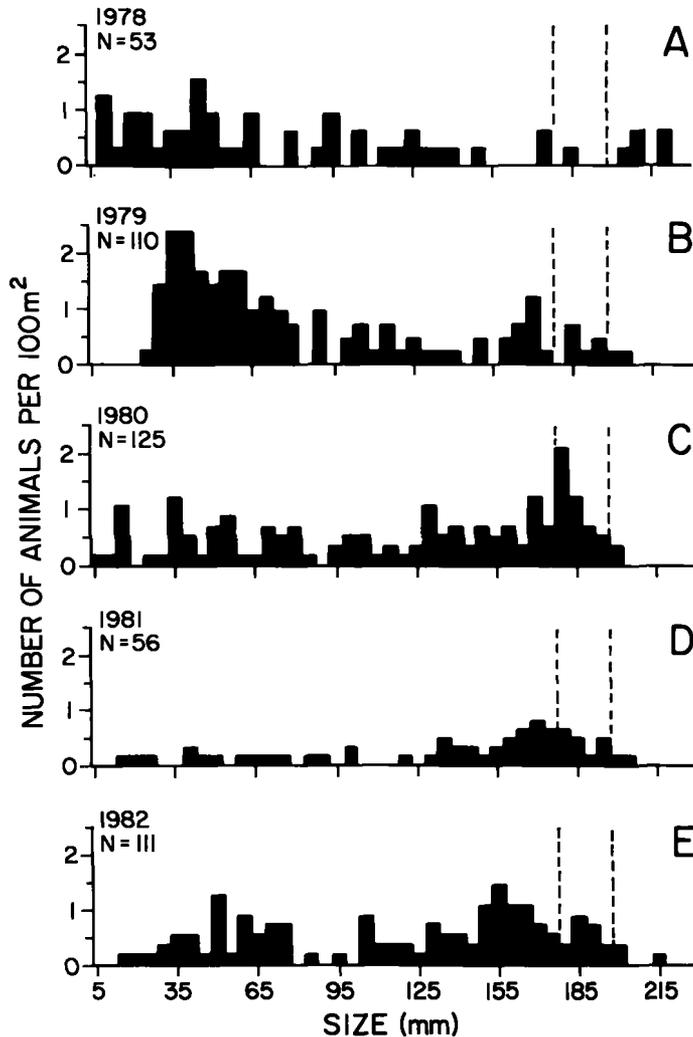


FIGURE 2.—Size-frequency distributions of red abalones recovered in the destruct quadrats by year, 1978–82. The data were scaled for differences in effort between years as follows. Each 5 mm size category for each year was divided by the respective total number of animals found for that year and then multiplied by the density for that year to yield a density at each 5 mm size category for that year. As the resulting numbers are small, each entry was multiplied by 100. The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

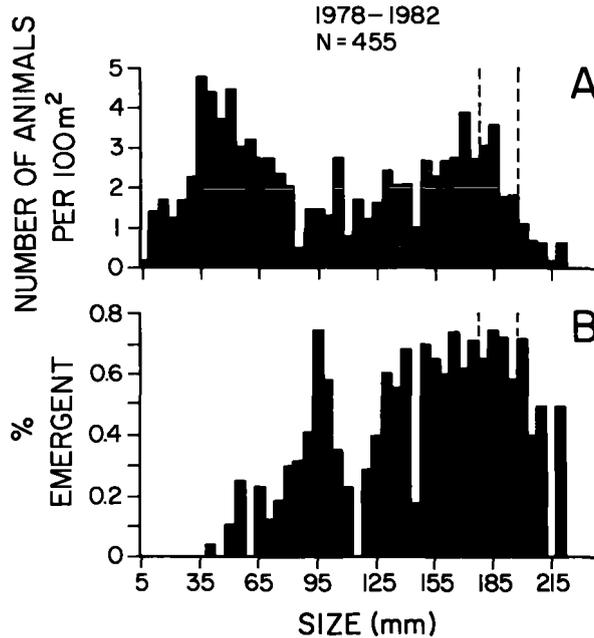


FIGURE 3.—Size-frequency distribution of red abalones found in the destruct quadrats summed for 1978–82. The scaled data from Figure 2 were summed across each 5 mm size category (A). Proportion of the total number of abalones found in the destruct quadrats which were emergent, visible to a diver without turning rocks or the use of a light, as a function of size class. These data were also scaled for differences in effort between years (B). The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

Yield-Per-Recruit Analysis

A program was written to calculate yield-per-recruit from equation 10.20 of Ricker (1975). Asymptotic weight W_{∞} was set to 1,500 g, based on length-weight data collected from Johnsons Lee in 1974 (CDFG, unpubl. data), and an L_{∞} of 201 mm. Maximum age λ was arbitrarily set to 25. K was set to 0.269, based on the tagging results (Haaker fn. 3). Two values of natural mortality rate M were used: 0.10 and 0.15, based on the results of this study.

To obtain isopleth diagrams, the instantaneous fishing mortality rate F was varied systematically from 0.0 to 2.0. The minimum size at first capture was varied from 140 to 200 mm.

Yield estimates were also made for pink abalones. Doi et al. (1977) reported growth parameters for males and females from two sites. We used the values for females from Cedros: $L_{\infty} = 186.0$ mm, $K = 0.233$, and $t_0 = 0.096$. These authors estimate that $M = 0.35$ at that site. We used this value and also $M = 0.20$ based on the estimated survival curve

from Tutschulte (1976, p. 250). W_{∞} was set at 1,216 g, based on the biometric data of Doi et al. (1977). Minimum size was varied from 100 to 180 mm, and F from 0.0 to 2.0.

Fecundity

Egg-per-recruit analysis requires knowledge or an estimate of the way that average fecundity varies with length. Because the procedure compares egg production under specified conditions with egg production in the unfished condition, the absolute number of eggs is not required; only the form of the relation is important.

Four sets of red abalone fecundity data were examined. These were Giorgi and DeMartini (1977), two sets from Ault (1982, 1985), and a set furnished by E. E. Ebert⁴. The first set of data in Ault (1982, 1985) was from a field collection; the second was from laboratory-conditioned animals.

⁴E. E. Ebert, Marine Culture Laboratory, California Department of Fish and Game, Monterey, CA 93940, pers. commun. 1986.

Table 2 shows the regression constants from the predictive regression of the natural logarithm of fecundity on the natural logarithm of length for each data set, and the range of lengths encompassed by each data set. Because the methods were widely different among the various sets and because the absolute numbers of eggs were not considered important, the four sets were combined in the following way. Each data set was scaled by dividing the observed number of eggs by 1 million times the number of eggs predicted for a length of 125 mm, from Table 2. The length 125 mm was chosen because it was most nearly common to all four data sets. The constant 1 million was used to minimize distortion when taking natural logarithms of the scaled data. Then the predictive regression of the natural logarithm of fecundity on the natural logarithm of length was calculated using data from all four sets. The constants obtained are also shown in Table 2.

The validity of this procedure was tested by using the egg-per-recruit model described below and comparing results from each of the fecundity regressions in Table 2. Results obtained using $M = 0.15$, $F = 1.0$ and 2.0, and minimum legal sizes of 179 and 191 mm are also shown in Table 2. The low variation between estimates using different fecundity relations, and the general similarity of the isopleths, allowed us

to conclude that egg-per-recruit analysis was not sensitive to our treatment of the fecundity data.

Egg-Per-Recruit Analysis

In egg-per-recruit modelling, one wishes to compare the egg production of a fished population with that of the equilibrium virgin population. The model described here is a simple, deterministic, age-structured model that allows individual variability in length around mean length-at-age. Thus cohorts can be partially recruited to the fishery.

The unfished population is considered first. The number of females of a particular size within a cohort of an unfished population is represented as $NV_{t,j}$, where t indexes cohort age and j indexes length. Each length h_j lies within one of the J intervals

$$(h_j - w/2, h_j + w/2); \quad j = 1, J$$

where $h_j = h_1 + (j - 1)w$ is the midpoint of the j th interval and each interval has width w . If N_0 is the abundance of females at age zero, the female abundance of each cohort in the unfished population is

$$NV_{t,j} = N_0 \exp(-Mt) \quad (1)$$

TABLE 2.—Fecundity analysis.

Predictive linear regression constants for equations relating fecundity to length in the four data sets described in the text. The equations are

$$\ln(\text{fecundity}) = a + b \ln(\text{length})$$

where length is in mm. The final set of constants describes the equation for the combined data - see text for the method used.

Data set	Range of lengths	<i>a</i>	<i>b</i>	<i>n</i>
Ault (1982, 1985) field-conditioned	112-194	-12.991	5.329	22
Ault (1982, 1985) lab-conditioned	65-182	-6.555	4.283	13
Ebert (text fn. 4)	42-83	-3.482	3.722	11
Giorgi and DeMartini (1977)	134-199	-16.572	6.1557	25
Combined data		-7.672	4.518	71

Results of egg-per-recruit modelling using the regression estimates above. Natural mortality rate was set to $M = 0.15$. Fishing mortality rate F and minimum legal size (MLS) were varied as shown. Results are expressed as percentages of egg production in the virgin population.

Data set	<i>F</i> = 1.0		<i>F</i> = 2.0	
	MLS = 179	MLS = 191	MLS = 179	MLS = 191
Ault (1982, 1985) field-conditioned	44.5	71.0	41.9	69.5
Ault (1982, 1985) lab-conditioned	48.9	73.8	46.5	72.5
Ebert (text fn. 4)	51.7	75.5	49.3	72.2
Giorgi and DeMartini (1977)	41.3	68.7	38.6	67.2
Combined data	47.9	73.1	45.4	71.8

where M is the instantaneous natural mortality rate. (The dot subscript indicates a summation over all j , i.e.,

$$NV_{t..} = \sum_{j=1}^J NV_{t,j}$$

and similarly

$$NV_{..j} = \sum_{t=1}^{\lambda} NV_{t,j}$$

where λ is the maximum age attained.) The mean length-at-age L_t can be described by the von Bertalanffy growth curve:

$$L_t = L_{\infty} \{1 - \exp[-K(t - t_0)]\}. \quad (2)$$

It is assumed that lengths-at-age are normally distributed around their mean, and that standard deviations vary with age in the manner proposed by Fournier and Breen (1983):

$$SD_t = a + b \sqrt{t} \quad (3)$$

where a and b are constants. If lengths-at-age are normally distributed around their mean in the unfished population, the probability that an individual in cohort t will be found in length interval j is

$$Q_{t,j} = \frac{1}{SD_t \sqrt{2} \pi} \int_{h_j}^{h_{j+1}} \exp[-(h - L_t)^2 / 2 SD_t^2] dh. \quad (4)$$

This was evaluated numerically.

Equations (2) to (4) could be used to describe a continuous growth process. For computational tractability, this model evaluates these relations only at integer values of t . This is equivalent to assuming that growth occurs yearly in one instantaneous increment; or alternatively that all fishing mortality occurs instantaneously when t assumes an integer value.

The number of individuals in all cohorts of the unfished population in length interval j is

$$NV_{..j} = \sum_{t=1}^{\lambda} Q_{t,j} NV_{t..} \quad (5)$$

Length-specific fecundity can be described by

$$f_j = c h_j^d \quad (6)$$

where c and d are regression constants and f_j is the

number of eggs produced by a female of length h_j . If spawning is assumed to occur once annually when t assumes an integer value, total egg production by an equilibrium population of females not subjected to fishing is described by

$$E_{\max} = \sum_{j=m}^J NV_{..j} f_j \quad (7)$$

where h_m is the length at first maturity. E_{\max} is calculated with appropriate parameter values and with a fixed arbitrary value for N_0 .

The model is now extended to include fishing mortality acting on all individuals whose length is equal to or greater than a minimum legal size h_R . The number of individuals at a particular size and age in the fished population will be denoted by $N_{t,j}$. It is assumed that no individuals are recruited to the fishery before age 1, so that

$$N_{1..} = N_0 \exp(-M). \quad (8)$$

In this and all subsequent cohorts, the number of individuals less than legal size will be the same as in the virgin population and can be determined as follows. The proportion of prerecruits in the virgin population is given by

$$QPR_t = \frac{1}{SD_t \sqrt{2} \pi} \int_0^{h_R} \exp[-(h - L_t)^2 / 2 SD_t^2] dh. \quad (9)$$

The number of prerecruits in each cohort is thus

$$NPR_{t..} = QPR_t NV_{t..} \quad (10)$$

and the number of individuals exposed to the fishery is

$$NR_{t..} = N_{t..} - NPR_{t..} \quad (11)$$

The overall survival rate of this cohort over one year will be determined by natural mortality acting on the prerecruits, and by both natural and fishing mortality on the recruits:

$$S_t = [(NPR_{t..} / N_{t..}) \exp[-M]] + [(NR_{t..} / N_{t..}) \exp[-(F + M)]] \quad (12)$$

Beginning with cohort 1, the abundance of successive cohorts can be determined:

$$N_{t..} = N_{t-1..} S_{t-1..} \quad (13)$$

The number of individuals in any cohort t and length interval j can now be determined if a further assumption is made. It is assumed that the length distribution of all recruited individuals within a cohort t is a truncated normal distribution, whose mean is L_t as described by Equation (2). In reality, the recruited segment of an older cohort will comprise several groups of individuals, each group having been exposed to fishing for a different length of time. Thus the length distribution of recruits in a cohort is unlikely to be normal. However, it is not possible to specify their distribution without specifying how varying annual length increments are distributed among individuals in a cohort. This is complex and requires further assumptions, so instead we have made the simplifying assumption described. We believe that the results are not sensitive to this assumption.

The number of individuals in each cohort t and each length interval j is given by

$$N_{t,j} = NV_{t,j} \quad j < R \quad (14)$$

$$N_{t,j} = Q_{t,j} NR_{t..} / (1 - QPR_t) \quad j \geq R$$

and total annual egg production is

$$E = \sum_{t=1}^{\lambda} \sum_{j=m}^J N_{t,j} f_j \quad (15)$$

Initial trials showed that this model is not unduly sensitive to the choice of a and b in Equation (3). The model was run with the same growth parameters used in the yield-per-recruit analysis; $\lambda = 25$; a and b in Equation (3) were set at 8.0 and 0.025 based on inspection of Figure 3; c and d in Equation (6) from the combined analysis in Table 2; and h_f was set to 50. It is assumed that male and female growth rates are the same. This may not necessarily be the case (Doi et al. 1977; Shepherd and Hearn 1983), but we have no information on sexual differences in growth of red abalones. F , M , and the minimum legal size h_R were all varied in the same way as in the yield-per-recruit analysis.

Egg-per-recruit analyses were also made for pink abalones, using the same growth data from females used in the yield-per-recruit analysis. The fecundity relation was obtained from Tutschulte (1976). It was assumed that the number of eggs is proportional to weight (2,078 eggs per gram whole weight in mature females); and that weight is proportional to length:

$$\text{weight (g)} = 2.66 \times 10^{-5} \text{ length (mm)}^{3.24}.$$

Lambda was set at 25; in the absence of data, a and b in Equation (3) were set to the same values as for red abalones; M was set at 0.2; and minimum size and F were varied as for yield-per-recruit analysis.

Simultaneous Analysis

Results from the yield- and egg-per-recruit analyses were combined in a third analysis to examine the relative performance of each combination of minimum size and fishing mortality rate (Breen 1986). Results from each of the previous two analyses are rescaled and then simply multiplied together:

$$SV = (Y/Y_{\max}) EPV \quad (16)$$

where SV is the "strategy value" of a particular combination of minimum size and fishing mortality rate, and takes values from 0 to 100; Y is the yield-per-recruit at that combination; Y_{\max} is the maximum yield-per-recruit; and EPV is transformed value of egg-per-recruit, given by

$$EPV = 0.0 \quad E < 20.0 \quad (17)$$

$$EPV = (3.333 E) - 66.6667 \quad 20.0 < E < 50.0$$

$$EPV = 100.0 \quad E > 50.0$$

where E is the egg production at that combination, expressed as a percentage of the egg production in the unfished situation. The relation of Equation (17) is designed so that when egg production is less than 20% of the virgin egg production, SV is zero; when E is greater than 50% of virgin egg production, SV is equal to the scaled value of yield-per-recruit. The values 20% and 50% are chosen as the values below which most managers would consider egg production to be dangerously low and above which egg production is probably adequate to maintain the stock, respectively.

This analysis was also carried out for pink abalones.

RESULTS

Field Studies

Population Structure

The size-frequency distributions of red abalones recovered in the destructively sampled quadrats

from 1978 through 1982 are illustrated in Figure 2. The size-frequency distributions are significantly different (G test, $P < 0.001$). By inspection, it is apparent that 1978 and 1979 are dominated by smaller animals. The best year for settlement (defined as young-of-the-year or ≤ 31 mm) was 1978 (Table 3), when the settlement rate was about three times the average of the other four years. These animals form a prominent mode in 1979 but the mode is not distinguishable in 1980.

the method of Pennington (1983). Assuming no changes in density between years, all data were combined with appropriate weighting for sample size differences to generate average densities of 0.179 m^{-2} ($\text{SE} \leq 0.066$) for the total number of abalones, 0.027 m^{-2} ($\text{SE} \leq 0.013$) for sport minimum legal sized, and 0.005 m^{-2} ($\text{SE} \leq 0.0035$) for commercial minimum legal-sized animals. Due to unestimable correlation between annual data, standard errors are given in terms of an upper bound. Despite intensification of the red sea urchin fishery during

TABLE 3.—Results from the destructively sampled quadrats, 1978–82.

	1978	1979	1980	1981	1982
Number of m^2 sampled	330	360	600	630	570
Red abalones					
Average density (m^{-2})	0.164	0.265	0.217	0.086	0.197
Standard error	0.049	0.161	0.065	0.032	0.049
Young of the year ≤ 31 mm abalones					
Average density (m^{-2})	0.036	0.019	0.017	0.005	0.011
Standard error	0.019	0.010	0.010	0.004	0.006
Percent total population	22.6	6.4	8.0	5.4	5.4
Sport-legal (≥ 178 mm) abalones					
Average density (m^{-2})	0.018	0.022	0.045	0.020	0.026
Standard error	0.009	0.014	0.021	0.008	0.009
Percent sport legal	11.3	7.3	21.6	21.4	14.4
Commercial-legal (≥ 197 mm) abalones					
Average density (m^{-2})	0.015	0.003	0.002	0.003	0.004
Standard error	0.009	0.003	0.002	0.002	0.003
Percent commercial legal	9.4	0.9	0.8	3.6	2.7
Red sea urchins					
Average density (m^{-2})	2.612	1.836	2.107	1.830	2.868
Standard error	0.780	0.406	0.616	0.667	0.537
Purple sea urchins					
Average density (m^{-2})	0.655	3.536	5.440	4.465	7.830
Standard error	0.177	1.767	1.300	1.407	1.400

The densities of different size categories of red abalones and of red and purple sea urchins in the destruct quadrats for 1978 through 1982 are presented in Table 3. There were no significant changes in the densities of the total number of abalones, young-of-the-year, sport legal minimum (≥ 178 mm), or commercial legal minimum (≥ 197 mm) sized animals based on 95% confidence intervals around the mean densities. Unequal sample sizes between years and the large number of quadrats with no abalones precluded analysis by ANOVA or the Kruskal-Wallis test. By separating those quadrats that contained abalones from those in which no animals were found, a conditional distribution for the nonzero valued samples could be proposed and tested. Several tests of normality did not reject the hypothesis that the natural log of the nonzero values is normally distributed. Annual total average densities and their variances were then estimated by

this period (Kato and Schroeter 1985), there was no change in red sea urchin density (Kruskal-Wallis test, $0.05 < P < 0.01$). In contrast, there was a significant increase in purple urchin density (Kruskal-Wallis test, $P < 0.001$).

Abalones occupy different microhabitats as their length increases (Cox 1962; Shepherd 1973, Tegner and Butler 1989), and microhabitat selection affects vulnerability to fishing (Witherspoon 1975). The proportion of emergent abalones from the destruct quadrats (1978–82 pooled, $n = 455$) is plotted in Figure 3 as a function of size class. There is an increase in percent emergent with increasing size which appears to level off at about 150 mm and 70% emergent and then decline as the animals attain legal size and emergent animals are apparently fished. Thus a substantial proportion of the largest animals in the population remain cryptic. Nevertheless, the low proportion of the population constituted

by animals of commercial legal size or larger (Fig. 2, Table 3) suggests that fishing pressure is very intense and that fishermen are searching for cryptic abalones. Thirty-five percent of the total number of abalones in the destruct quadrats were emergent (yearly range: 25–50%).

Total, sport-legal, and commercial-legal densities of emergent abalones were calculated from the combined results of the destruct and nondestructively sampled quadrats. Again inspection of the 95% confidence intervals around the yearly means suggests that there were no significant changes in density over the five years studied despite the fourfold larger sample sizes and correspondingly smaller standard errors. The mean density of the total number of abalones from these quadrats was 30% of the mean total density determined from the destruct quadrats, comparable to the 35% of the destruct quadrat animals which were emergent. The density of emergent, commercial legal-sized animals ranged from one to three per 1,000 m², again suggesting that Johnsons Lee is intensely searched. In contrast, the density of emergent sport legal-sized red abalones ranged from 10 to 23 per 1,000 m². The size-frequency distribution of emergent abalones from both the destruct and nondestruct quadrats is illustrated in Figure 4.

The high variance in the density estimates can be ascribed to two factors. First, a substantial proportion of the rocky substrate was a very flat, pave-

ment-like surface often covered with a thin layer of silt. This surface supports *Macrocystis* and rarely large red abalones, but not small or intermediate-sized animals. Second, the distribution of abalones at Johnsons Lee was highly contagious in all years sampled. The variance to mean ratio was calculated as an index of dispersion and the significance of departures from unity tested with χ^2 , and for large samples ($n > 31$), with the normal variable (Elliot 1971). In each case the χ^2 value was highly significant ($P < 0.005$). In 1979, for example, 63% of the total number of abalones found in the destruct samples were in one quadrat.

Habitat Considerations

Cox (1962) reported that abalones prefer areas where there is sand, and Shepherd (1973) recognized the importance of sand patches and channels as areas for the movement and accumulation of algal drift. A χ^2 analysis was conducted to determine whether red abalones were concentrated in the rock/sand areas or uniformly distributed between the rock and rock/sand habitat types (Table 4). On the scale of the 15 m² quadrats, red abalones, both emergent and nonemergent, did not show a preference for either habitat type. In contrast, both red and purple sea urchins were found in habitat classified as rock more often than expected.

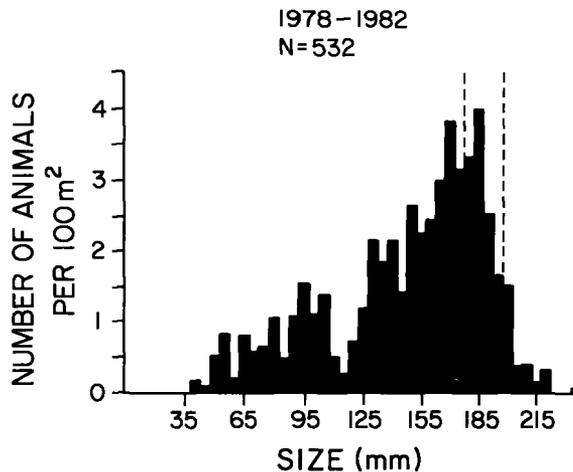


FIGURE 4.—Size-frequency distribution of emergent red abalones found in the destruct and nondestruct quadrats, 1978–82. The data were scaled for differences in effort between years. The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

TABLE 4.—Habitat analysis. The distribution of red abalones and red and purple sea urchins between rock and rock/sand habitats are tested against the null hypothesis that the animals are uniformly distributed between these two habitat types. Data are pooled for 1978–82.

Destruct quadrats				
Habitat sampled	Number of m ² sampled		Percent	
Rock	1,095		45.6	
Rock/sand	1,305		54.4	
	Emergent red abalones	χ^2 analysis	Non-emergent red abalones	χ^2 analysis
Rock	73	0.051	135	0.003
Rock/sand	84	n.s.	160	n.s.
	Red sea urchins	χ^2 analysis	Purple sea urchins	χ^2 analysis
Rock	3,116	285	6,766	937
Rock/sand	2,357	**	4,519	**
Non-destruct quadrats				
Habitats sampled	Number of m ² sampled		Percent	
Rock	2,715		42.9	
Rock/sand	3,615		57.1	
	Emergent red abalones	χ^2 analysis		
Rock	168	0.001		
Rock/sand	223	n.s.		

** = significant at $\alpha = 0.001$.

n.s. = not significant.

Predator Populations

We censused all known or suspected macroscopic abalone predators (O'Connell 1953; Pilson and Taylor 1961; Cox 1962; Burge et al. 1975; Tutschulte 1976; Ambrose 1984; Hines and Pearse 1982; Tegner and Butler 1985, 1989) on the transects; the results are presented in Table 5. The most abundant predators were sea stars. Of the suite of species encountered at Johnsons Lee, only two are known to

feed on healthy abalones. Breen (1980) reported that *Pycnopodia helianthoides* occasionally fed on *H. kamtschatkana*, and D. Parker⁵ observed a *Pycnopodia* eating two juvenile (38 and 46 mm) red abalones at Johnsons Lee in 1977. Schiel and Welden (1987) recently reported observations of *Pycnopodia* predation on juvenile red abalones in the laboratory.

⁵D. O. Parker, California Department of Fish and Game, 330 Golden Shore, Long Beach, CA 90802, pers. commun. 1986.

TABLE 5.—Predator densities for 1978–82.

Predator	Number per hectare (SD) for the year				
	1978	1979	1980	1981	1982
<i>Pycnopodia helianthoides</i>	250 (433)	83 (118)	112 (130)	107 (145)	83 (92)
<i>Astrometis sertulifera</i>	17 (35)	—	17 (51)	4 (18)	—
<i>Cancer</i> spp.	—	42 (56)	42 (69)	12 (30)	26 (79)
<i>Octopus</i> spp.	8 (25)	21 (52)	38 (57)	4 (18)	9 (26)
<i>Scorpanichthys marmoratus</i>	—	—	12 (30)	4 (18)	9 (38)
<i>Semicosyphus pulcher</i>	34 (96)	30 (41)	55 (55)	45 (54)	58 (53)

Astrometis sertulifera consumed abalones up to 80 mm in aquaria experiments (Tegner and Butler 1989). Night dives indicated that the *Pycnopodia* densities in Table 5 are considerably underestimated; juveniles are cryptic during the day. *Astrometis* also tends to be nocturnal or at least crepuscular (MacGinitie and MacGinitie 1968; Tegner pers. obs.). Because many small, empty abalone shells were found without any shell damage, and because juvenile *Pycnopodia* and *Astrometis* are common in cryptic habitats where juvenile abalones live, we suspect that these starfishes may be important predators of small haliotids. *Pycnopodia* and *Pisaster giganteus* both attacked recently replanted adult abalones from the tagging study but *Pisaster* does not appear to be a predator of unstressed abalones (Feder 1959, 1963; Tegner and Butler 1989).

In a study of the gut contents of 87 sheephead collected near San Diego, we found that molluscs are an important part of the diet of smaller fishes and found a juvenile red abalone (15 mm) in one gut (Tegner unpub. data). Thus sheephead predation on unstressed and undisturbed animals is probably rare, but these fishes are attracted to divers and probably take juvenile abalones under the spine canopies of red urchins as the urchins are fished. Sheephead and bat rays do attack recently replanted abalones (Burge et al. 1975; Tegner pers. obs.).

Some predators characteristic of the warmer areas of the southern California Bight were rare or absent at Johnsons Lee. Bat rays, which feed primarily on emergent adult abalones (Tegner and Butler 1989), were attracted to transects on two occasions in 1978 and once in 1981 after the fish had been counted. Spiny lobsters, *Panulirus interruptus*, and sheep crabs, *Loxorhynchus grandis*, have been observed to prey on juvenile and mid-sized red abalones on the Palos Verdes Peninsula (Tegner and Butler 1985). No lobsters and only one sheep crab was seen during the 5 yr course of this study. As all of our visits took place during June and July, we would not have observed any seasonal variation in predator populations.

Patterns of Shell Production

The size-frequency distributions of red abalone shells from 1980 to 1982 and 1984 are illustrated in Figure 5. If we assume a constant rate of mortality independent of age (Fournier and Breen 1983), then we would expect a decline in the frequency of shells with increasing size above the size range where shells are likely to be destroyed by predators. Large modes from about 170 to 195 mm especially

in 1980 and 1981 do not fit that expectation. These modes almost certainly reflect bar cut mortality, fatal injuries to abalone soft tissues caused by the collecting tool (Burge et al. 1975; Tegner 1989). In 1981 and 1982, this increase in shell frequency can be resolved into two modes: one just below sport minimum size (178 mm) and one immediately below commercial minimum size (197 mm). The larger number of shells found in 1980 represents years of accumulation; this was the first year in which the tagging area was sampled.

The large shell collections of 1980–82 were examined for evidence of cause of death. Some kinds of shell damage could be ascribed to specific predator types (Cox 1962; Hines and Pearse 1982; Tegner and Butler 1985, 1989) or to the boring sponge *Cliona celata* (Cox 1962; Abbott and Haderlie 1980). Other shells were undamaged or the damage was ambiguous and probably sometimes the result of deterioration after death; for these animals the cause of death was unknown. Fifty-three shells (including data from 1984) had *Octopus* spp. drill holes but, as these cephalopods do not drill all their prey (Tutshulte 1976; Ambrose 1984), this is a minimal estimate of the importance of octopus predation to this abalone population. Red abalones appear to attain a refuge in size (shell thickness) from octopus predation; only three of the drilled shells were larger than 125 mm (Fig. 6). The most common pattern of shell damage was the scratches, chipped edges, and small breaks along the growth edge characteristic of rock crab (primarily *Cancer antennarius* but may include *C. productus*) predation (Cox 1962). Rock crabs appear to be able to handle the full size range of red abalones at Johnsons Lee. *Cliona* was found in a wide size range of red abalone shells but only in very large shells did the degree of infestation appear sufficient to have contributed to the abalones' death by weakening the shells (Cox 1962). The size-frequency distributions of the mortalities attributed to octopuses, rock crabs, and *Cliona* are significantly different from each other (Kolmogorov-Smirnov tests, $P < 0.01$). Bat ray predation can be recognized from shells fractured into large pieces (Tegner and Butler 1989). A small number of mortalities (7–10 per year) could be ascribed to this predator. No shells were found with the acid-etched appearance characteristic of cabezon, *Scorpaenichthys marmoratus*, predation (Hines and Pearse 1982). For the years 1980–82 (tagging area only, $n = 986$), octopuses account for a minimum of about 4% of the mortalities, rock crabs 21%, *Cliona* infestation 6%, and bat rays 2%, and 67% of the deaths could not be assigned on the

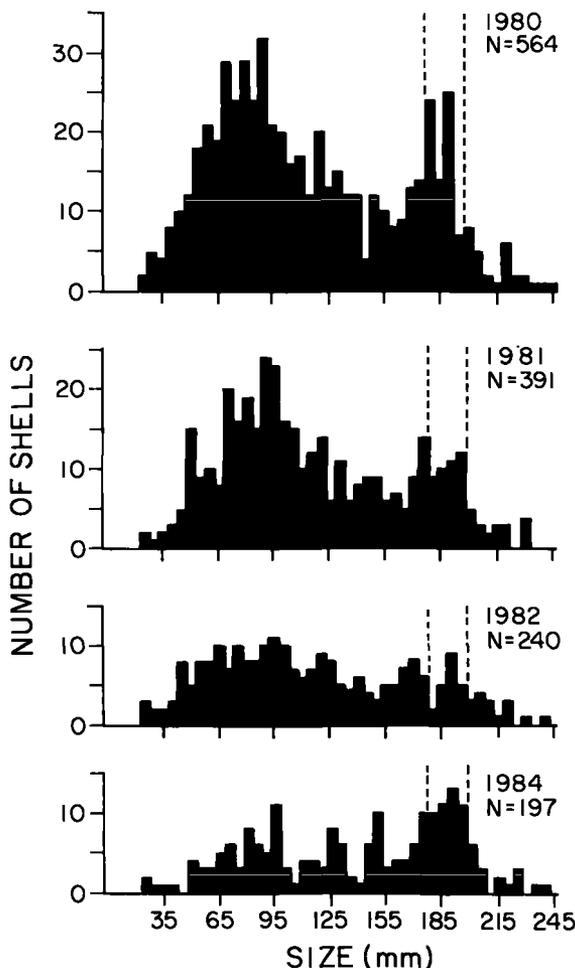


FIGURE 5.—Size-frequency distributions of red abalone shells recovered in the tagging area by year, 1980–82 and 1984. The dashed lines indicate sport (178 mm) and commercial (197 mm) legal minimum sizes.

basis of shell damage. Inspection of the size-frequency distributions of the shells for 1980–82 (Fig. 5) suggests that a minimum of about 10% of the total mortalities during this period can be ascribed to bar cut injuries.

Mortality Rate

Using the values shown in Table 1, total mortality rate Z estimates ranged from 0.165 to 0.222. Sensitivity of the estimate to initial conditions and parameters was tested over a broad range of values; the results from some of these tests are shown in Table 6. The estimate was fairly robust to changes in the assumed number of age classes, increasing

as the number of age classes increased. Tagging results suggest that 15 years are required on average for red abalones at Johnsons Lee to reach 200 mm (P. Haaker fn. 3), so we favor estimates based on 16 age classes. Forcing the method to give an estimated L_{∞} consistent with the tagging results had little effect. The estimate was sensitive to constraints on the standard deviations of length, increasing as larger standard deviations were permitted. Removing the first two age classes from the estimation led to decreased estimates, but removing further age classes indicated a robust estimate near 0.180. We conclude that the best estimate of total mortality, based on realistic constraints, is $Z = 0.180$.

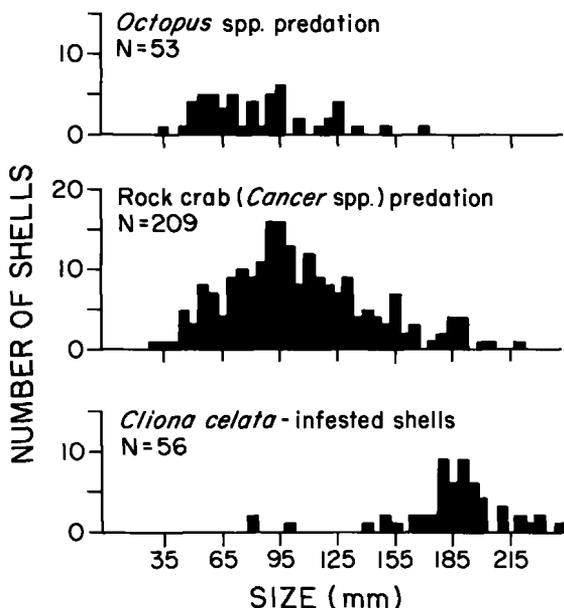


FIGURE 6.—Size-frequency distributions of red abalone shells recovered in the tagging area 1980–82 which could be attributed to a specific predator.

Natural mortality rate must be less than the estimated Z . Commercial exploitation begins at 197 mm, recreational exploitation at 178 mm, and mortality associated with exploitation (bar-cutting) reduces the number of individuals smaller than legal size (Fig. 5). The method used here suggests a value of M around 0.15.

Yield-Per-Recruit Analysis

Isopleth diagrams for red abalones using $M = 0.10$ and 0.15 are shown in Figure 7A and B respectively. The minimum size associated with the maximum yield-per-recruit estimate is sensitive to the value of M used: it is 176 mm when $M = 0.10$, and 164 mm when $M = 0.15$. Both sets of estimates show the pattern described by Breen (1986): except at very low values of F , the yield estimates are not sensitive to variation in F ; conversely at low values of F , the yield estimates are insensitive to variation in minimum size.

For pink abalones, yield isopleths are shown in Figure 7C and D. The minimum size producing the greatest estimated yield is very sensitive to the estimate of M . If $M = 0.35$, as Doi et al. (1977) suggested, then the best minimum size is 116 mm; if

TABLE 6.—Effect of changing input parameters and initial conditions on estimated total mortality rate Z in red abalones, using the data in Figure 3 and Table 1. T is the value of the objective function; the goal is to minimize this function in conjunction with realistic mortality rate estimates. Unless specified, bounds in the first and last standard deviations of lengths-at-age for the first and last cohorts are 7.5 and 8.5.

Effect of varying the total number of age classes							
NK	16	15	14	13	12		
Z	0.196	0.194	0.193	0.182	0.165		
T	481	483	486	492	500		
Effect of releasing constraints on estimated mean length of the last age class							
		Constrained	Unconstrained				
	Z	0.196	0.195				
	T	481	481				
Effect of changing upper and lower bounds on the estimated standard deviations of lengths-at-age around the mean length-at-age. Bounds on the first line are those for the first cohort; those on the second line are for the last cohort. The asterisk indicates when the model was not actually constrained by the bound.							
	Bounds	7.5, 10.5	7.5, 15.5	1.0, 15.5			
		7.5, 10.5	7.5, 15.5	1.0, 15.5*			
	Z	0.203	0.222	0.222			
	T	332	236	236			
Effect of varying the age of the first age class, N_{FULL} , included in the calculation of total mortality rate ($NK = 16$)							
N_{FULL}	1	2	3	4	5	6	7
Z	0.206	0.196	0.180	0.180	0.177	0.181	0.174
T	481	481	480	480	480	480	480

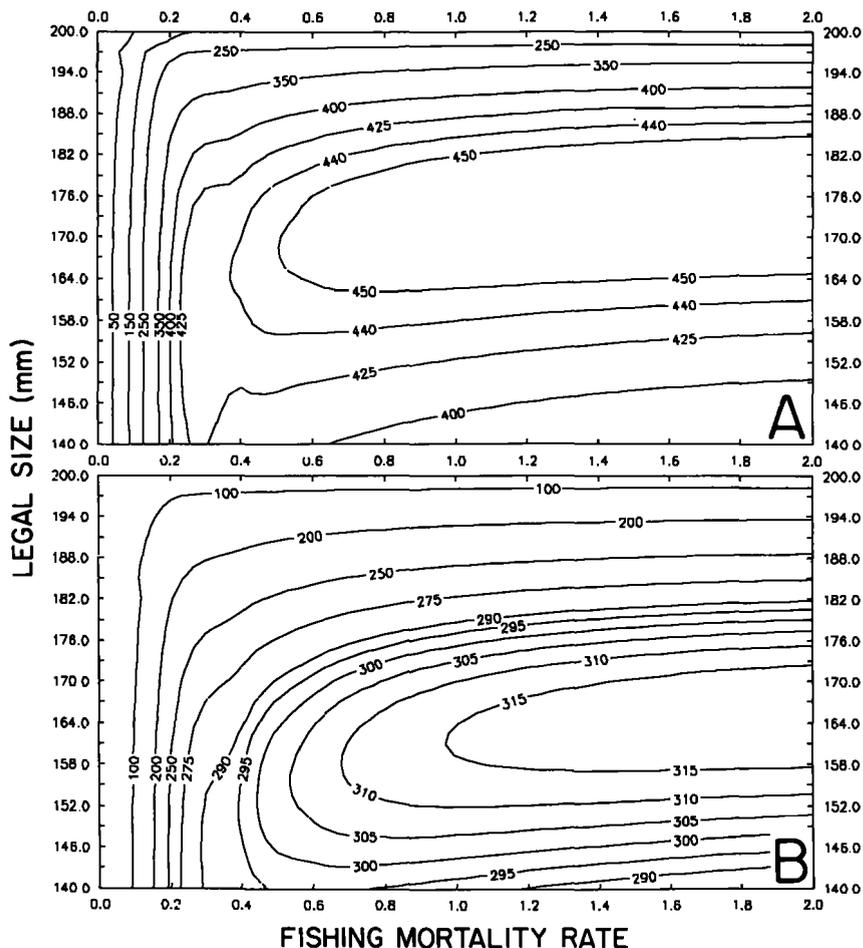


FIGURE 7.—Yield-per-recruit (g) as a function of minimum legal size and instantaneous fishing mortality rate, determined by the method of Beverton and Holt (Ricker 1975). For red abalones, parameters were $K = 0.269$, $L_{\infty} = 201$ mm, $W_{\infty} = 1,500$ g, and $M = 0.10$ (A) and $M = 0.15$ (B).

$M = 0.20$, then the best minimum size is 140 mm. Both are substantially lower than the present minimum legal size.

Fecundity

Regression constants for the power curves relating fecundity to shell length in the four data sets are shown in Table 2. This table also shows the constants from the combined analysis, which were used in egg-per-recruit analysis.

Egg-Per-Recruit Analysis

Results for red abalones using $M = 0.10$ and M

$= 0.15$ are shown in Figure 8A and B respectively. Three points should be noted. First, egg production estimates are sensitive to the natural mortality rate, decreasing as M decreases. Second, even at the smaller recreational size limit and very high rates of fishing, egg production estimates are reasonably high. With $M = 0.10$, egg production by abalones below the recreational size limit should be more than 35% of the virgin population egg production. At higher values of M , large size limits, or lower fishing intensities, the estimate is higher. At the more realistic point of using $M = 0.15$, $F = 1.0$, and the recreational size limit, egg production would be 48%. Third, combinations of F and size limits that produce the best yield-per-recruit lead to

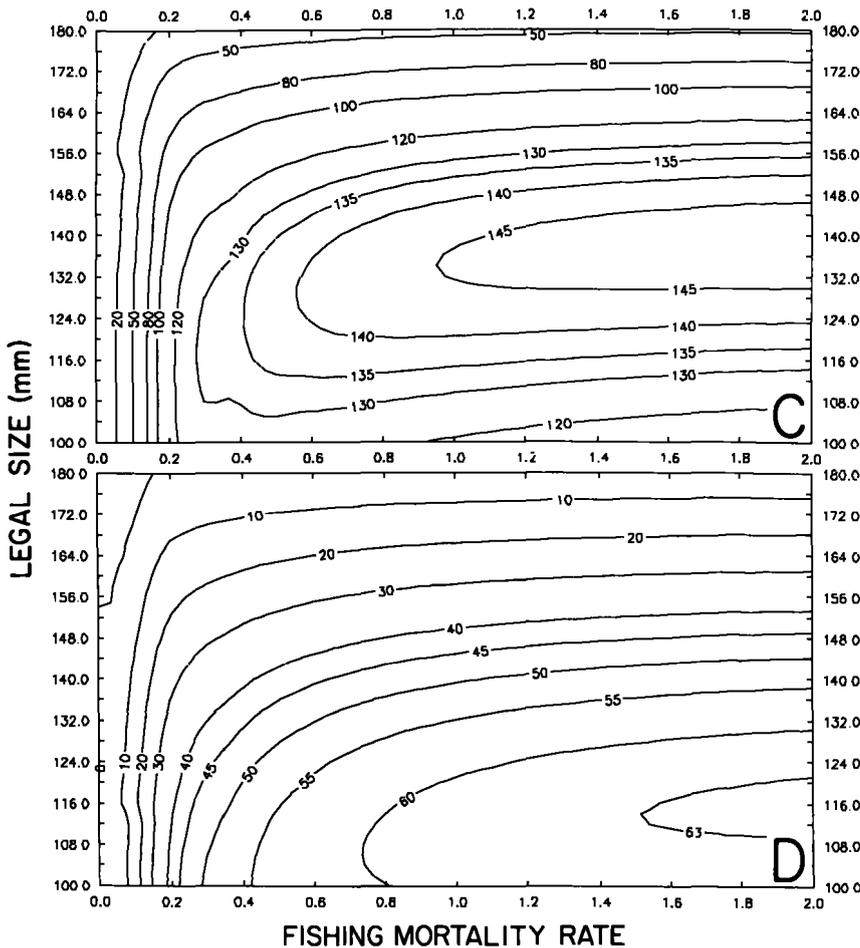


FIGURE 7.—Continued—For pink abalones, parameters were $K = 0.233$, $L_{\infty} = 186$ mm, $W_{\infty} = 1,216$ g, and $J = 0.20$ (C) and $M = 0.35$ (D).

35% egg production at $M = 0.10$ and 27% at $M = 0.15$.

For pink abalones, egg production estimates are shown in Figure 8C and D. At $F = 2.0$ and the present minimum legal size of 152 mm for recreational harvesters, egg production estimates for $M = 0.20$ and $M = 0.35$ were 51% and 75% respectively.

Simultaneous Analysis

For red abalones, isoline diagrams illustrating values of SV are shown in Figure 9A and B, using $M = 0.10$ and $M = 0.15$ respectively. The curves connecting best combinations of fishing mortality

and minimum legal size are quite similar. The optimum combination occurs at high fishing mortality rates; at a minimum legal size of 188 mm when $M = 0.10$ and at 182 mm when $M = 0.15$. Note that when F is greater than 0.3, SV is sensitive to the choice of minimum legal size but not to F ; while at low values of F the reverse is true.

Results for pink abalones are shown in Figure 9C and D. With both estimates of M , the optimum SV occurs when $F = 2.0$; however, the best minimum legal size is very sensitive to estimated M . If $M = 0.35$, the best minimum legal size is 128 mm; if $M = 0.20$, the best minimum legal size is 152 mm (the present sport minimum size).

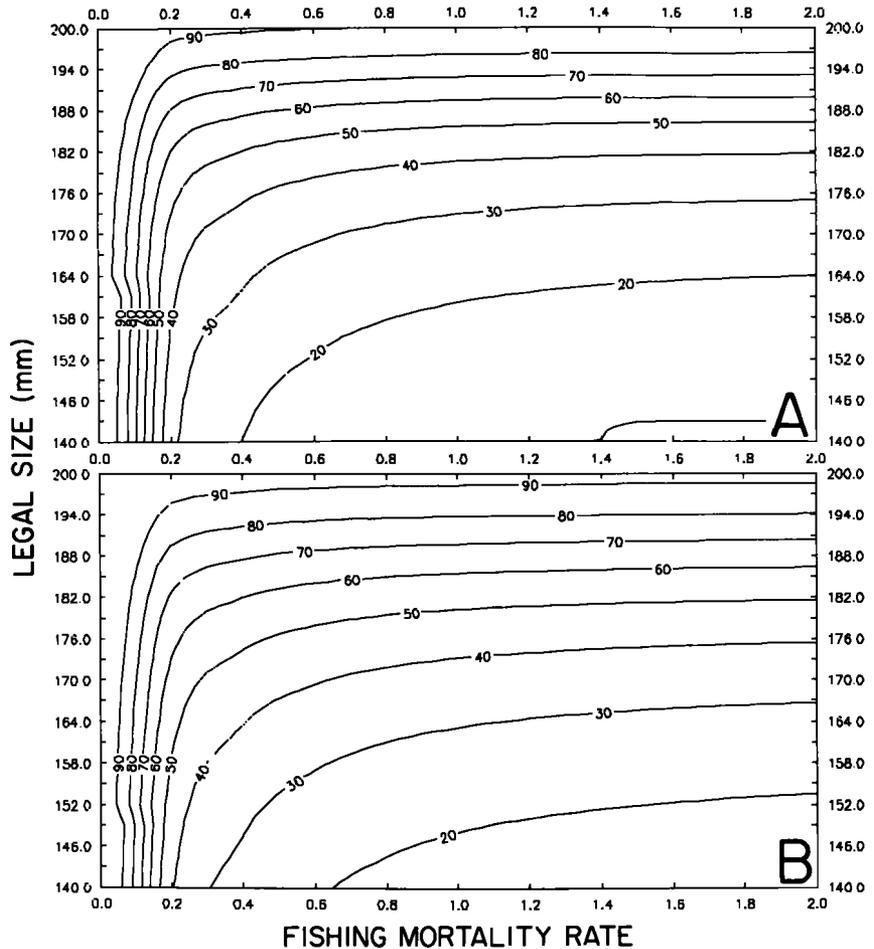


FIGURE 8.—Eggs per recruit, expressed as a percentage of the eggs that would be produced by an

DISCUSSION

Field Studies

Johnsons Lee was a "very good" abalone bed in the late 1940s, an era when strong winds and currents created problems for fishermen with heavy dive gear (Glenn Bickford⁶). More recent assessments suggest that this situation continued; commercial fishermen considered Johnsons Lee to be one of the best red abalone beds in southern California from the early 1970s through 1983. The number of commercial-legal individuals dropped sharply after 1983, perhaps as a result of the El Niño of

1982–84, but the productivity was high again in 1987 (Austin Apodaca⁷). The history of Johnsons Lee cannot be traced beyond this qualitative level; there are no previous quantitative studies and the scale of CDFG block landing records is too large. For the years 1978 through 1982, a period for which our data suggest that the population density was stable, we estimate that the total number of red abalones in our 36 ha study site, assuming an average density of 0.179 abalones per m² and that 80% of the habitat was suitable for abalones based on the average transect rejection rate, was 51,552 animals (SE \leq 19,008). This included 7,776 (SE \leq 3,744) sport minimum legal-sized individuals and 1,440 (SE \leq

⁶G. Bickford, P. O. Box 729, Morrow Bay, CA 93442, pers. commun. 1987.

⁷A. Apodaca, 1702 Mountain, Santa Barbara, CA 93101, pers. commun. 1987.

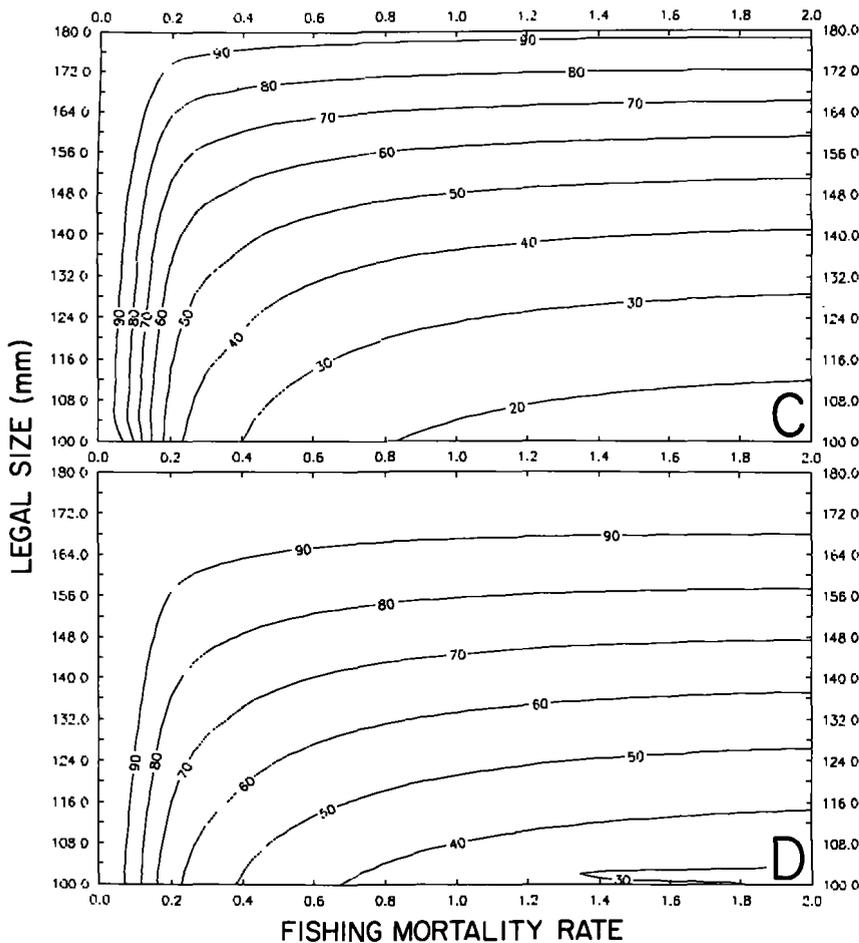


FIGURE 8.—Continued—unfished cohort. See text for procedure. Parameters were all identical with those used in Figure 6.

1,008) commercial minimum legal-sized animals. The density of red abalones at Johnsons Lee is comparable to the average 0.2 abalones per m^2 found in the Victorian fishery for *H. rubra* (Beinssen 1979a) but considerably less than recent mean densities of *H. kamtschatkana* in British Columbia (Breen 1986).

Bar cuts have been a continuing problem in California abalone fisheries. Burge et al. (1975) reported market sampling data from 1974, indicating that commercial divers cut 8.6% of their red abalone catch. They felt that the bar cut rate of picked and replaced sublegal animals was likely to be higher because of their more cryptic nature. These authors found a nearly 60% mortality rate in laboratory studies of *H. rufescens* with a 13 mm cut in the foot; mortality is likely to approach 100% in

the presence of predators. They presented size-frequency data for pink, *H. corrugata*, and green, *H. fulgens*, abalones which showed decreases in the number of animals within 6 mm of commercial minimum legal size. While the decreases could have been caused by sport harvest or commercial take of sublegal animals, Burge et al. (1975) believed that they were caused largely by the mortality of picked and replaced short abalone. Figures 3A and 4 illustrate similar marked drops in the number of red abalones within 5 mm of both sport and commercial minimum legal size. The size-frequency distributions of shells (Fig. 5) provide strong evidence for mortality of picked and replaced short abalones by sport and especially commercial fishermen. The approximately 10% of total observed mortality which we have attributed to bar cuts is especially damaging to fish-

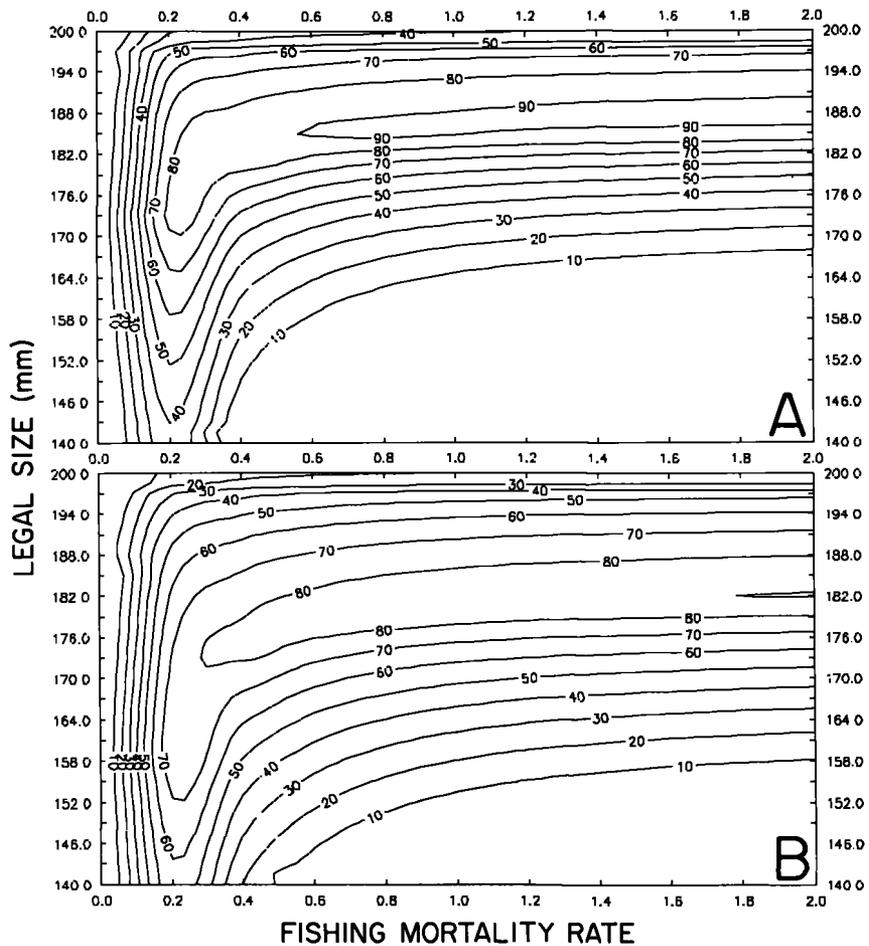


FIGURE 9.—Relative values of various combinations of minimum size limit and fishing mortality rate, using the procedure described in the text and the parameters of Figure 7. Values have a range of

able stocks because animals this size would have a high probability of attaining legal size.

One of the goals of the limited entry legislation, which went into effect in 1977, was to reduce the turnover rate of fishermen; presumably fewer divers with more experience would reduce the frequency with which sublegal abalones are picked and replaced. Similarly, the reduction in the sport daily bag limit in 1976 was accompanied by a requirement that the first four legal-sized abalones taken must be kept; exchange for larger abalones was forbidden (Cicin-Sain et al. 1977). The shell size-frequency data (Fig. 5) clearly indicate that bar cut mortality is continuing in the 1980s. The low density of commercial-legal minimum-sized abalones (Table 3) suggests that bar cuts also reflect intense pressure on a scarce resource; many animals must be picked and

measured to sort out the few legal-sized individuals (Burge et al. 1975).

Sea stars are the most abundant of the potential abalone predators at Johnsons Lee, but their role is not clear. A large study of sea star foraging at the Hopkins Marine Life Refuge in central California reported no observations of abalone being eaten by sea stars (Harrold 1981 reported in Hines and Pearse 1982) but *Pycnopodia* is known to have very different diets in different habitats (Mauzy et al. 1968). Montgomery (1967) demonstrated that young (<100 mm) red abalones exhibit strong flight responses to *Pycnopodia* in aquaria experiments. Similarly, Hines and Pearse (1982) observed that contact with *Pycnopodia* caused abalones to rapidly move 5–20 cm deeper into crevices at Hopkins. This behavior, plus the large number of juvenile

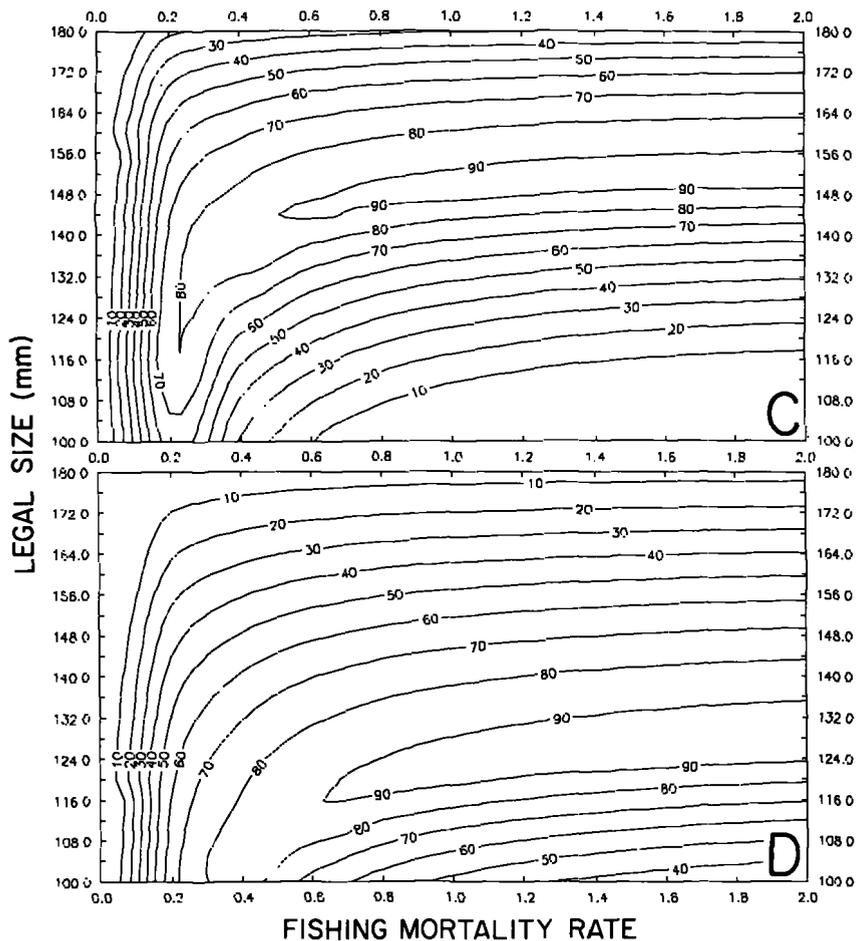


FIGURE 9.—Continued—0–100 with 100 representing maximum yield-per-recruit and at least 50% of possible egg production.

abalone shells without any shell damage and the abundance of juvenile *Pycnopodia* and *Astrometis* in cryptic juvenile abalone habitat, leads us to suspect that these sea stars are important predators of small haliotids. Conversely, there is more support for the role of rock crab predation (Cox 1962). The 21% mortality assigned to *Cancer* predation in this study was the largest proportion which could be unambiguously assigned to any predator, and this value is undoubtedly an underestimate of rock crab importance as many cases of minor chipping were considered ambiguous. Given their nocturnal activity pattern and tendency to bury in the sand by day (Ricketts and Calvin 1968), the observed densities of *Cancer* (Table 5) may be considerably underestimated.

The predation patterns observed at Johnsons Lee

varied considerably from the results of a study of juvenile (<100 mm) red abalones on the Palos Verdes Peninsula (Tegner and Butler 1985), a mainland site about 160 km southeast of Santa Rosa Island. Here 33% of the shells ($n = 325$) found in a year-long study had octopus drill holes and 34% were ascribed to crustacean predation, primarily by spiny lobsters. The octopus density at Johnsons Lee is much lower than at Palos Verdes, but these cephalopods may still be important predators of juvenile red abalones; 9 of 21 shells recovered from a small-scale seeding (size range 22–52 mm) experiment conducted at Johnsons Lee in 1977 had been drilled (Tegner unpub. data). The relatively low level of octopus predation at Johnsons Lee may also reflect the larger average size of individual animals at this location; Figure 6 suggests that red abalone attain

a refuge in size from this predator at about 125 mm.

Hines and Pearse (1982) present size-frequency and density data for several red abalone populations in central California under different predation regimes which contrast markedly with the results from Johnsons Lee. The Hopkins Marine Life Refuge has been within the sea otter range for many years and the abalone population is dependent on an extensive crevice refuge. The density of emergent abalones was higher than at Johnsons Lee (0.18 m^{-2} vs. 0.06 m^{-2}) but the effects of intense otter predation are apparent in the population structure; the average size of emergent red abalones was 8 cm (vs. 15 cm at Johnsons Lee) and of shells was 10 cm (vs. 11 cm). At a site north of the otter range, the average size of red abalones was 18 cm, more than twice the size at Hopkins, and an average shell size of 21 cm was found at an intermediate site recently invaded by the mammals (Hines and Pearse 1982). These rather dramatic differences underscore the importance of studying abalone population dynamics in a biogeographic context.

In his monograph on California abalones, Cox (1962) reported that the San Miguel Island fishery produced predominantly red abalones while all the other Channel Islands produced mostly pink abalones. (These were the only two haliotids fished at this time in California.) In this 5 yr study, only three live pink abalones were found on the transects at Johnsons Lee, all in 1978. Unpublished CDFG block landing records for 1983 indicate that the red abalone harvest exceeded the take of pink abalones on Santa Rosa, San Nicolas, and Santa Cruz Islands as well as on San Miguel Island. The reason for this apparent shift in species composition is not clear. Growth and larval survival of *H. rufescens* are optimal in cooler temperatures than for *H. corrugata* (Leighton 1974), but there is no evidence of a cooling trend since the early 1960s sufficient to produce this shift. As both species have been fished actively since the mainland south of Point Conception and the Channel Islands were reopened to commercial harvest in 1943 (Cox 1962), it is unlikely that competition was important. Pink abalones are more susceptible to bar cuts (Burge et al. 1975), a factor which would affect both the yield to the fishery and the reproductive potential of the stocks. The shift may reflect relative differences in egg production or larval dispersal potential. The average red abalone landings for 1981-86 represented 17% of the average landings for this species for 1950-70. For pink abalones, which were not affected by sea otter predation during this time period, this figure was

3%, suggesting that *H. corrugata* is less resilient to fishing pressure.

Mortality Rate

Our mortality rate estimate for *H. rufescens* is higher than Smith's (1972) estimate (an annual turnover rate of 0.05), that was based on a length-frequency sample of large animals in northern California. Our estimate is consistent with the direct observations of survival at Hopkins (Hines and Pearse 1982), but lower than estimates of turnover rate from empty shell production obtained in the same study. These authors favor the estimate based on shell production, considering that their choice of sites for making direct observations may have been biased toward good refuges from predation. Without predation by sea otters, mortality rates in the two studies would appear to be similar.

The Fournier and Breen (1983) method can only estimate total mortality rate, which in this study is based on both exploited and preexploited segments of the population. We estimate natural mortality as being less than this estimate. A second problem is the assumption that each cohort resulted from an initial cohort of the same size. The data (Fig. 2) do not support this assumption but the effects of variable recruitment are minimized by combining data for several years in a standardized form.

Natural mortality rate may vary with age in some molluscs, and such variation is important in making estimates from age-structured models (Appeldoorn 1988). Mortality may be higher for the first two age classes of red abalones, because we obtained higher mortality estimates when these were included (Table 6). After the first two age classes mortality estimates were stable, supporting the assumption that natural mortality is independent of age.

Implications for Management

Several authors consider abalones to be particularly susceptible to "recruitment overfishing" sensu Gulland 1973 (e.g., Harrison 1969; Sainsbury 1977; Mottet 1978; Breen 1980). Some reasons for this belief are as follows (see also Harrison 1986). Low adult natural mortality rates lead to dense "top-heavy" populations with a high proportion of large adults. Because fecundity increases exponentially with length, much of the breeding capacity of the population can be concentrated in these large individuals. Diving is an extremely efficient harvesting method on open substrate types (e.g., Beinssen 1979b). Abalones have a high unit value, so economic

self-regulation of the fishery does not occur. Thus the fishery can remove a high fraction of the accumulated stock in a short time (e.g., Kojima et al. 1978), leading to greatly reduced breeding potential and thence recruitment failure. Although this mechanism is an attractive explanation for unexpected declines in exploited abalone populations, Harrison (1986) pointed out that recruitment failure has never been convincingly demonstrated in an abalone fishery. Such a demonstration would be difficult, because the stock-recruit relationship is not known for any abalone species. Without knowing the relation between stock and subsequent recruitment, one cannot know how much breeding stock must be maintained. However, egg-per-recruit analysis can provide clues as to whether egg production is adequate (e.g., Sluczanowski 1986; Praeger et al. 1987).

For California red and pink abalones, the decline in fishery landings may have many causes (Burge et al. 1975; Cicin-Sain et al. 1977; Tegner 1989). The declines occurred after large increases in fishing pressure, so one is tempted to conclude that recruitment overfishing as described above was a contributing cause. Our analysis does not support that conclusion, at least for red and pink abalones in southern California. Our egg-per-recruit analyses suggest that, with the present minimum legal sizes, egg production would be maintained at healthy levels for both species, even at very high fishing mortality rates. For red abalones, with our estimate of $M = 0.15$, egg production would be maintained at about 50% even if the population were fished down to the recreational size limit. It is hard to imagine recruitment failure happening at this level of egg production.

We conclude that simple recruitment overfishing is not a satisfactory explanation for the decline in red and pink abalone landings. Some possible qualifications should be noted. First, the results of egg-per-recruit analysis are sensitive to the growth parameters used as input. Underestimation of either L_{∞} or the Brody coefficient leads to overestimation of relative egg production. Because growth in abalones varies greatly among habitats (Sainsbury 1982; Shepherd and Hearn 1983; Breen 1986) and varied considerably from year to year in this study (P. Haaker fn. 3), egg production analyses based on growth data from one site might not reflect the situation at other sites. The paucity of published growth data for California abalones, and the importance of such data in assessing the fishery, point to a need for further growth studies.

Second, the mortality caused by handling sublegal

abalones (picking and replacing them) has the same effect on egg production as a reduction in minimum legal size. Thus estimates of egg production at the present minimum legal size are known overestimates. However, egg production is still good well below the present legal sizes (Fig. 8C, D) so this problem is unlikely to affect our conclusion.

Third, simple analyses such as this ignore spatial and ecological complexities. At a particular site, fishing mortality might be much higher than the population-wide rate. If dispersion of larvae is limited, as Prince et al. (1987) suggested, locally intense harvesting events could cause long-lasting changes in local populations. Another complexity is that abalones may aggregate to spawn (Shepherd 1986), thus becoming far more vulnerable to fishing mortality than the nonbreeding population. Finally, populations reduced to low densities may not be able to realize their potential egg production because of reduced fertilization efficiency.

Although this study does not support the idea that recruitment overfishing has been a serious problem, it does support the idea that reproductive factors should be considered along with yield estimates when fishing strategies are developed. The strategies which lead to the best yields in red abalones (Fig. 7A, B) are strategies that lead to lower egg production than others (Fig. 8A, B). As Sluczanowski (1984, 1986) found for South Australian abalones, egg production can be greatly increased with small reduction in yield-per-recruit by choosing different combinations of minimum legal size and fishing mortality rate.

If recruitment overfishing cannot be invoked to explain declining landings, what happened? Some of the explanations offered by Burge et al. (1975) may remain valid. Many sublegal abalones may be killed by handling. In at least the early years of the fishery, the stock was being "fished down" as years of accumulated production were removed; the landings may have been higher than sustainable levels during this period. However, it seems unrealistic to argue that the fishing down process lasted from 1950 through 1970 (e.g., Cox 1962). Sea otters have effectively removed abalones from parts of the coast that contributed to the fishery. Fishing closures have eliminated access to other areas.

Direct and indirect environmental effects may also be partly responsible, especially for species near the end of their range, such as pink abalones on the northwestern Channel Islands. Abalones do not necessarily spawn every year (e.g., Sainsbury 1982). Temperature appears to be a major controlling influence on spawning (Pearse 1978; Uki and Kikuchi

1984). Food availability is also involved; when massive storms removed virtually all the kelp from Palos Verdes in the winter of 1983, green abalones missed their normal late spring spawning (Tegner and Dayton 1987). Temperature also effects larval survival (Leighton 1974); thus variability in the reproductive success of abalones could be intimately related to variations in water temperature regimes. Paine (1986) observed that purple sea urchins settled successfully only four times in 20 years on the outer Washington coast and suggested that settling success was associated with warm-water events. Similarly, Tegner and Dayton (1987) found strong settlement of pink abalones into what had been a red abalone bed at Palos Verdes and simultaneously found a near absence of young reds during the 1982-84 El Niño. Shepherd et al. (1985) suggested that poor settlement of *H. scalaris* is associated with cool-water temperatures. Similar suggestions are made by Hayashi (1980) and Forster et al. (1982). Interannual variability in surface currents will have a direct effect on larval transport; larvae which end up in unsuitable habitat are not likely to contribute to fishable stocks. This has been demonstrated for several finfishes (Walford 1938; Nelson et al. 1977; Bailey 1981; Sinclair et al. 1985). The transport anomalies associated with El Niños (Chelton et al. 1982) may be responsible for purple urchin settlement in Washington and the pink abalone event described above.

An indirect effect of hydrographic events is proposed by Sakai (1962) who found a high correlation between abalone landings and harvests of the seaweed *Undaria pinnatifida*. Sakai suggested that seaweed growth, and consequently abalone production, varies with the strength of the Kurile (Oyashio) Current. Similarly, El Niños in California involve a reduced California Current and increased transport of warmer waters from the south (Chelton et al. 1982). During the major El Niño of 1957-59, Cox (1962) reported that abalone growth practically ceased, body tissues appeared to shrink, gonad development was minimal, and there was poor recruitment to the fishery. When Johnsons Lee was sampled in 1984, few animals were found above sport minimum legal size and growth was the lowest observed during this study (P. Haaker fn. 3). It is now clear that the warm water associated with these events leads, in addition to kelp mortality, to a sharp decrease in the nitrogen content of algal tissues; such kelp is probably an inadequate food to support herbivore growth or reproduction (Tegner and Dayton 1987).

The egg-per-recruit model we used was determin-

istic, whereas breeding success is stochastic. Future work should try to measure the degree of variation in settlement and recruitment success, then evaluate population responses with a simulation model incorporating the variability observed. Studies of this type have shown that stochastic variation in recruitment creates difficulties in rebuilding depleted stocks (e.g., Archibald et al. 1983). If abalone larval settlement is only occasionally successful, maintenance of the population may require a much larger breeding stock than otherwise expected.

The importance of environmental effects in explaining declining abalone abundance is evident in several studies where abundance or recruitment declined in the absence of a fishery. Breen (1986) and Sloan and Breen (1988) reviewed the evidence for *H. kamtschatkana* in British Columbia. Sainsbury (1982) observed fluctuating recruitment in an unfished population of *H. iris* in New Zealand. In the English Channel Islands, *H. tuberculata* has undergone strong fluctuations in recruitment and abundance, even where not exposed to a fishery (Forster et al. 1982). If unexploited stocks undergo major fluctuations in recruitment caused by environmental effects, then the fluctuations in heavily exploited stocks may be severe under the same conditions. As Gulland (1973) pointed out, "if the fluctuations in year class strength, independent of the abundance of adults, are large, then it is possible that a serious collapse of the stock can occur before the need for management is recognized and appropriate measures taken."

To manage abalones properly, fishery managers would need to know the relation between breeding stock size, which they can manipulate through regulation, and subsequent stock size. If there were little relation, then the best strategy would be to maximize the yield from whatever recruitment occurs. At the other extreme, Prince et al. (1987) suggested a strong relation between local stock size and recruitment. In this case the manager must balance the need to maximize yield with the need to maintain good egg production, and the need to maintain resilience in the face of environmental uncertainty.

In the absence of better information, we suggest that prudent abalone management should follow the lead of Sluczanowski (1984, 1986) and adopt the goal of maintaining egg-per-recruit at the cost of some potential yield. Our results support Harrison's (1986) contention that the minimum size limit should be the basic management tool in meeting this goal, as fishing mortality rate is unlikely ever to fall below $F = 0.3$. To set appropriate size limits requires good information on growth patterns, fecundity and

breeding patterns, and natural mortality rates. Our study underscores the need for better data on California abalone species.

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