Variation in geographic stock area, catchability, and natural mortality of ocean shrimp (*Pandalus jordani*): some new evidence for a trophic interaction with Pacific hake (*Merluccius productus*)

Robert W. Hannah

Abstract: Interannual variation in geographic stock area, catchability, and natural mortality of age 2 ocean shrimp (*Pandalus jordani*) was investigated for the years 1980–1990, using commercial catch and logbook data. Stock area changed gradually from 1980–1990, but showed wide variation, demonstrating that an assumption of constant catchability is not valid for ocean shrimp. Stock area was positively correlated with total catch, suggesting that stock area increases roughly in proportion to shrimp abundance. The time series of fishing effort and effort per unit stock area were quite different, showing that fishing effort probably gives incorrect information on time trends in ocean shrimp fishing mortality. Natural mortality rates varied widely over the study period also and were positively correlated with the abundance of age 2+ Pacific hake (*Merluccius productus*), a known shrimp predator. The best correlations were between natural mortality rates and the number of age 2–7 Pacific hake. Hake abundance indices that included only age 3+ fish were not significantly correlated with shrimp natural mortality rates, suggesting that if a trophic interaction exists between these two species, it may be influenced by hake recruitment events.

Résumé : On a examiné la variation annuelle de l'aire géographique, de la vulnérabilité et la mortalité naturelle de la crevette océanique (*Pandalus jordani*) d'âge 2, de 1980 à 1990, sur la foi des statistiques sur les prises commerciales et des données contenues dans les livres de bord. De 1980 à 1990, l'aire de répartition du stock s'est modifiée graduellement mais d'une manière très variable, ce qui prouve la caducité de l'hypothèse de la vulnérabilité constante pour la crevette océanique. Une corrélation positive a été établie entre l'aire du stock et les prises totales, ce qui laisse supposer que l'aire du stock s'élargit à peu près proportionnellement à l'abondance. Les séries chronologiques de l'effort de pêche et de l'effort par unité dans l'aire du stock étaient passablement différentes, ce qui montre que l'effort de pêche donne probablement des informations fausses sur les tendances temporelles de la mortalité par pêche chez l'espèce. Les taux de mortalité naturelle variaient grandement, au long de la période, et une corrélation positive a été établie entre ceux-ci et l'abondance de merlu du Pacifique (*Merluccius productus*) d'âge 2+, un prédateur connu de la crevette. Les corrélations les plus certaines ont été établies entre les taux de mortalité naturelle et le nombre de merlus du Pacifique d'âge 2 à 7. On n'a pas établi de lien significatif entre les indices de l'abondance du merlu, qui visaient uniquement des poissons d'âge 3+, et les taux de mortalité naturelle de la crevette; donc, s'il existe une interaction trophique entre ces deux espèces, elle subit peut-être l'influence des épisodes de recrutement du merlu.

[Traduit par la Rédaction]

Introduction

The population dynamics of ocean shrimp *Pandalus jordani* have been investigated by a number of authors. Geibel and Heimann (1976), Zirges and Robinson (1980) and

PFMC (1981) present reviews of the early work on ocean shrimp. To date, attempts to model the ocean shrimp population have all relied on two important simplifying assumptions; constant catchability and constant natural mortality (Geibel and Heimann 1976; Hannah 1993). In the late 1960s, population estimates (Abramson 1968; Gotshall 1972) and commercial catch and effort data were used to estimate maximum sustainable yield via the Schaefer model (Abramson and Tomlinson 1972) for the shrimp beds in Pacific States Marine Fisheries Commission (PSMFC)

area 92 (Fig. 1). For a number of years the northern California ocean shrimp trawl fishery was managed by a quota, based on the estimate of sustainable yield from the Schaefer model. This management approach was abandoned when it became apparent that shrimp recruitment, abundance, catch per unit effort (CPUE), and age composition fluctuated widely, an indication that the underlying assumptions of the Schaefer model were probably not met, even approximately (Geibel and Heimann 1976).

Attempts to derive a stock–recruitment relationship for ocean shrimp have also met with little success. The early efforts, which focused on the area 92 population, did develop some recruitment estimates, but found no relation between spawning stock and recruitment (Geibel and Heimann 1976). I subsequently developed a recruitment index for ocean shrimp (Hannah 1993) based on catch and effort data from areas 82–92 (Fig. 1). Recruitment was shown to be strongly correlated with changes in sea level at the time of larval release, suggesting that early larval transport plays a major role in determining year class success. However, even after accounting for environmental variation, as recommended by Garcia (1983) and others, no relation between spawning stock and recruitment was found. The failure to demonstrate a stock–recruitment relationship is not unusual, especially for a shrimp stock. A variety of authors have pointed out that it is difficult to detect such relationships in stocks with high fecundity, high and variable natural mortality, or environmentally driven recruitment (Goodyear and Christensen 1984; Koslow 1992). However, the lack of success in detecting a stock–recruitment relationship for ocean shrimp could also be the result of more fundamental problems with the methods used. If catchability and natural mortality are highly variable for ocean shrimp, errors in the indices used could be obscuring an underlying relationship between stock and recruitment. The principal objective of this analysis is to attempt to determine how reasonable the assumptions of constant catchability and natural mortality are for ocean shrimp.

Several authors have also discussed the potential impact that the very large population of Pacific hake *Merluccius productus* might have on the ocean shrimp population. While Pacific hake feed primarily on euphausiids (Outram and Haegle 1972; Livingston and Alton 1982; Livingston 1983; Rexstad and Pikitch 1986), the work of Gotshall (1969) and Alton and Nelson (1970) demonstrate that Pacific hake can feed heavily on ocean shrimp at times. Despite the differences found between various studies in the prevalence of ocean shrimp in the diet of Pacific hake, several authors have suggested that the extremely large biomass of Pacific hake could still have major effects on the ocean shrimp population (Francis 1983; Rexstad and Pikitch 1986). Livingston and Bailey (1985), however, examined the available evidence and concluded that there was not strong evidence pointing to a major predator–prey interaction between Pacific hake and ocean shrimp. A second objective of this study is to further evaluate the link between ocean shrimp and Pacific hake by comparing the variation found in shrimp mortality rates with fluctuations in the abundance of Pacific hake.

Fig. 1. Location of commercial concentrations of ocean shrimp *Pandalus jordani* along the U.S. Pacific coast (shaded areas) and PSMFC statistical areas 72–92.
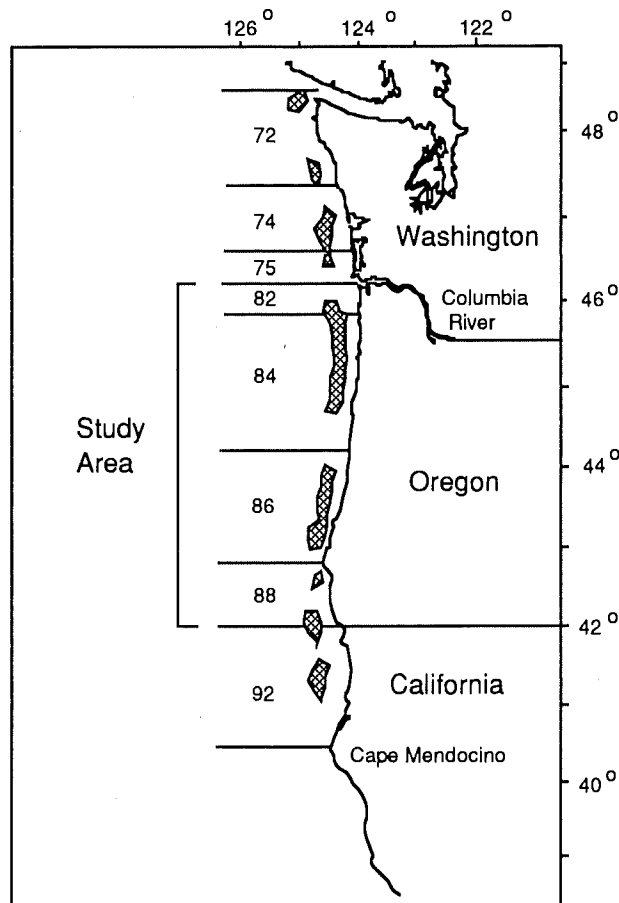
Materials and methods

Two primary data sets were used in this analysis of the shrimp population in PSMFC statistical areas 82–88 (Fig. 1). Commercial logbook data from landings made into Oregon ports, detailing the location and catch for individual hauls, were used to generate estimates of stock area for the years 1980–1990. Data on commercial fishery catch and effort, and biological samples of the commercial catch, both of which are compiled by PSMFC statistical area, were used to generate mortality rate estimates (Zirges et al. 1982; Oregon Department of Fish. and Wildlife (ODFW), unpublished data). The collection and analysis of biological samples from the commercial catch is described by Hannah and Jones (1991). In instances where catch and effort were noted for a particular area or month, but biological samples for age and size composition were missing, samples were used from adjacent months or areas. The use of sample data from adjacent months or areas was assumed to have minimal impact on estimates of catch at age, because strata with missing samples generally had very low levels of catch.

In this study, stock area was defined as the estimated area (ha) in which commercial quantities of ocean shrimp were located by the trawl fleet. For a number of reasons, the

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Table 1. Ocean shrimp stock area (ha), total catch (t), and the amount of catch and percentage of total catch included in the logbook data sets for PSMFC statistical areas 82–88, 1980–1990.

Year	Stock area (ha)	Total catch (t)	Catch included (t)	Percentage of total catch Included	Vessels included	Percentage of all vessels landing in Oregon
1980	310 081	9 981	2473	24.8	142	49.1
1981	330 998	8 676	2470	28.5	123	49.4
1982	281 340	6 392	1703	26.7	80	46.2
1983	152 646	1 702	520	30.6	52	40.0
1984	81 273	1 599	383	24.0	20	33.9
1985	193 841	5 137	2266	44.1	48	50.0
1986	366 126	11 460	4705	41.1	89	58.6
1987	384 967	18 918	5409	28.6	115	64.3
1988	409 237	17 221	5677	33.0	105	58.0
1989	552 781	21 291	9244	43.4	124	67.0
1990	466 236	11 137	5245	47.1	121	67.2

Note: Also shown is the number of vessels included in the logbook data sets and the included vessels as a percentage of all vessels landing ocean shrimp into Oregon ports, 1980–1990.

ocean shrimp trawl fishery is well suited to use commercial catch and effort data to estimate stock area. Fishing is unrestricted with respect to fishing area, and no catch quotas or trip limits are used to manage the fishery. Accordingly, vessels generally search for shrimp quite broadly and fish aggressively wherever concentrations of shrimp are located. It is very unlikely that sizable areas harboring commercial quantities of shrimp have gone unfished in the years included in this study. The haul data consisted of a large subsample of the available and usable logbooks, and covered all ports of landing and months of the year when shrimp fishing occurs. Vessels are required to keep a logbook of all fishing activity for ocean shrimp, and standard logbooks are provided by the management agencies. The methods used to keypunch, standardize, and error check the logbook information, as well as some of the errors that render individual trip logs unusable at times, are described by Starr et al. (1989) and Fox et al. (1992). To estimate stock area, the haul data were first transformed into a format suitable for mapping. This involved a series of steps. First, the tow start location data, which are recorded in LORAN-C or latitude and longitude coordinates, were converted into a rectangular coordinate system. The tow start location was used as the best approximation for the location of the tow, because it was assumed that fishermen began towing very near where they expected to obtain a good catch of shrimp. A standard geographical grid of 160-ha blocks was then constructed for the entire study area, using the computer program Spyglass Transform®. For each year, the CPUE for individual hauls was averaged by block, based on the start location for the haul. The number of blocks in which CPUE averaged greater than zero was multiplied by 160 ha to estimate stock area. Stock area estimates were also calculated separately for each statistical area. A threshold of zero CPUE was used because a low threshold mimimizes the effect of spatially

uniform changes in abundance on estimates of stock area (Swain and Sinclair 1994).

Winters and Wheeler (1985) have suggested that the relationship between CPUE, population size, stock area and the catchability coefficient is described by the equation

[1] $CPUE = paNA^{-b}$

with

[2] $q = paA^{-b}$

where, p is the proportion of fish within the sweep of the gear which will be captured (the elemental efficiency), A is the stock area, a is the area covered by a single sweep of the gear, b is a coefficient which describes how q will vary with stock area, N is the population size, and, q is the catchability coefficient. Accordingly, an assumption of constant catchability is equivalent to assuming that stock area is constant (Winters and Wheeler 1985; Paloheimo and Dickie 1964). Beverton and Holt (1957) recognized the same problem with catchability and stock area, but approached a solution in a different way. They treated catchability as a true constant, but recognized that it could only be constant if the spatial distribution of fish and fishing was uniform and constant over time. They redefined fishing effort as the "effective overall fishing intensity," a quantity which is "a weighted sum of the intensities in each subarea taking the local density of fish into account." This quantity will then be proportional to the coefficient of fishing mortality. While the treatment of the problem by Beverton and Holt (1957) is perhaps more thorough, in that it addresses problems caused by changes in the distribution of fish and fishing effort, the approach used by Winters and Wheeler (1985) is more useful here because this study is concerned specifically with the effect of changes in stock area.

Fig. 2. Estimated stock area (thousands of ha) for the ocean shrimp stock in the study area, 1980–1990.

Fig. 3. Linear regression of ocean shrimp stock area (thousands of ha) on the landed catch (t) of ocean shrimp from the study area, 1980–1990.
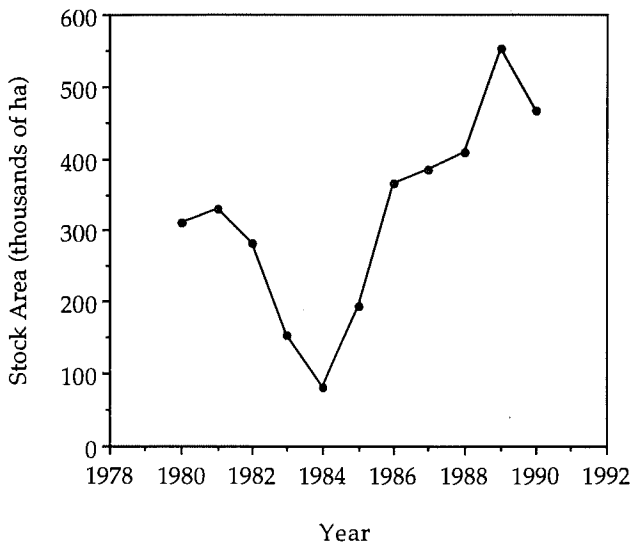
A simple inspection of the 1980–1990 estimates of stock area can be used to evaluate the validity of the constant catchability assumption for ocean shrimp. If stock area isn't constant, catchability won't be. However, to calculate annual values for natural mortality from estimates of total mortality, using the equation:

[3] $Z = qf + M$

where, Z is the average monthly instantaneous total mortality rate, f is the nominal fishing effort, and M is the average monthly instantaneous natural mortality rate, annual values for the catchability coefficient must be calculated, as well as estimates of the average monthly rate of total mortality. To calculate q from estimates of stock area, additional information is needed, specifically estimates of b, a, and p in Eq. 2 above.

An estimate of a was calculated using data from several sources. The average trawler in the ocean shrimp fleet is double rigged and fishes a combined footrope length of about 51 m (ODFW, unpublished data). Double-rigged effort is routinely converted to single-rigged equivalents using a multiplier of 1.6 (PFMC 1981). Based on discussions with net manufacturers and data from Watson et al. (1984) the spread ratio of ocean shrimp trawls was determined to be about 50%. Using an average tow speed of about 3.7 km/h, these data yield an estimate of 5.93 ha for the area swept by one single-rig-equivalent hour of fishing effort.

It was assumed that b in Eq. 2 above was equal to 1. This is equivalent to assuming that the catchability coefficient is inversely proportional to stock size (Paloheimo and Dickie 1964) and also that changes in stock area are directly proportional to changes in stock size (Winters and Wheeler 1985). It was unclear how this assumption might influence the variation in estimates of natural mortality. However, an attempt was made to test whether this assumption was reasonable. Since 1978, the annual catch in the ocean shrimp fishery has been dominated by age one shrimp; in
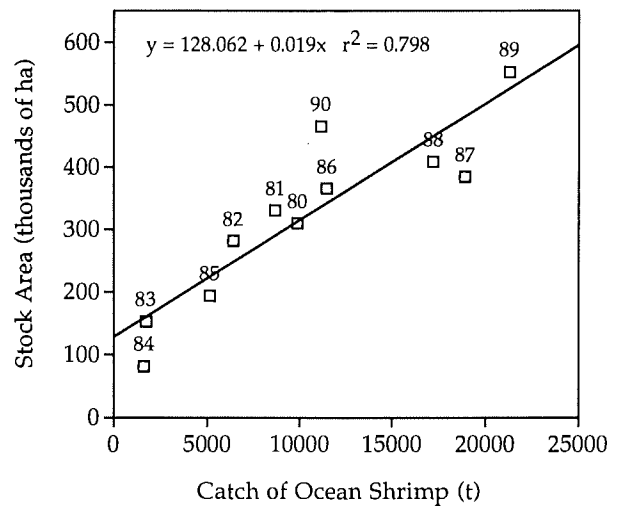
essence it has become a fishery on new recruits (Hannah and Jones 1991). Accordingly, for the ocean shrimp fishery in recent years, total catch may be a crude index to population size. To help evaluate the assumption that b is approximately equal to 1, I regressed annual catch against stock area to see if, in fact, changes in stock area have been proportional to changes in stock size.

Mortality rates were estimated, for the years 1980–1990, using a variant of the catch curve approach applied to age 2 ocean shrimp (Ricker 1975; Gotshall 1972). Age 2 shrimp from the study area are considered to be fully recruited to trawl gear (Lo 1978; ODFW, unpublished data). Age 1 shrimp are incompletely recruited to trawl gear in the first few months of each April–October fishing season. Prior to calculating CPUE values, fishing effort was standardized for single-rigged and double-rigged trawl vessels (PFMC 1981). Total catch and effort for the stock area were calculated by expanding the effort recorded in usable logbooks based on total catch for each port and month, including data from the states of California, Oregon, and Washington. Age 2 CPUE values (numbers of age 2 shrimp/single-rig trawl hour) were calculated for each of the four statistical areas, weighted by the proportion of the total stock area contained in that statistical area that year, and then summed (Beverton and Holt 1957). The weighting was used because the four areas differ in size, and the stock area inhabited by shrimp within a statistical area could vary between years. In using the catch-curve method to estimate mortality rates, it is assumed that catchability is roughly constant within the April–October season. For age 2 shrimp, this is a much more conservative assumption than assuming that catchability is constant over periods of years, especially in light of the argument of Winters and Wheeler (1985) that changes in stock area are related to changes in stock abundance. The natural logarithm of the summed age 2 CPUE values was then regressed against time, in months, for the period April through October. Each statistically significant linear regression ($p < 0.10$)

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Fig. 4. Geographical distribution of the ocean shrimp stock in 1980, 1984, 1985, and 1989. Each 160-ha block represents an area in which commercial vessels began a haul that resulted in nonzero CPUE for ocean shrimp.
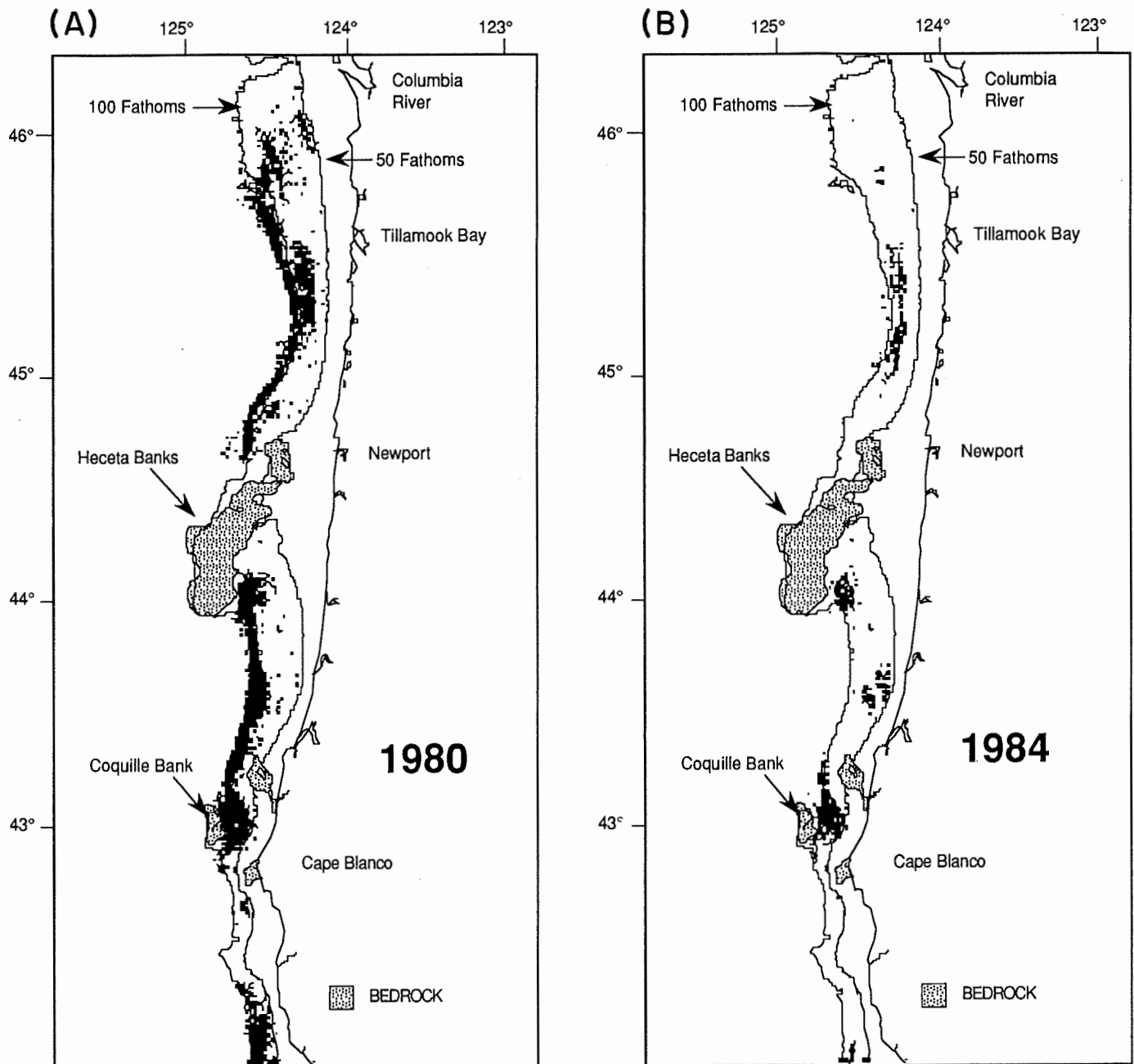

provided an estimate of the average monthly instantaneous total mortality rate for the April–October period.

No data were available to directly estimate p, the proportion of shrimp within the swept area that are captured by the gear. Accordingly, three values of p, covering a reasonable range for this parameter, were used. The values I used were 0.25, 0.50, and 0.75. It is unlikely that the elemental efficiency of shrimp gear is higher than 0.75, on average. Ocean shrimp migrate up off of the bottom at night (Pearcy 1970) and for this reason the trawl fishery is pursued only during daylight hours. However, Beardsley

(1973) demonstrated that ocean shrimp also rise off of the bottom in response to reduced light levels during the day, and can become unavailable to trawl gear, thereby probably reducing the average efficiency of trawl gear.

To evaluate the relationship between ocean shrimp natural mortality rates and the abundance of Pacific hake, simple linear regression was used. Data on hake abundance were obtained for the U.S. portion of the stock for the years 1960–1992 (Dorn et al. 1993; M.W. Dorn, Alaska Fisheries Science Center, Seattle Wash., unpublished data). The variables regressed against shrimp natural mortality
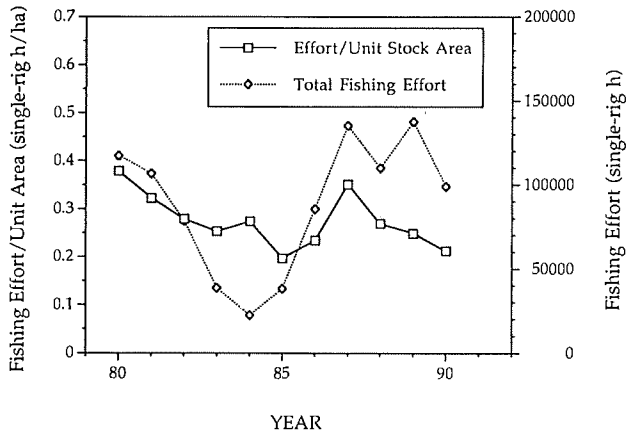
Fig. 4 (*concluded*).
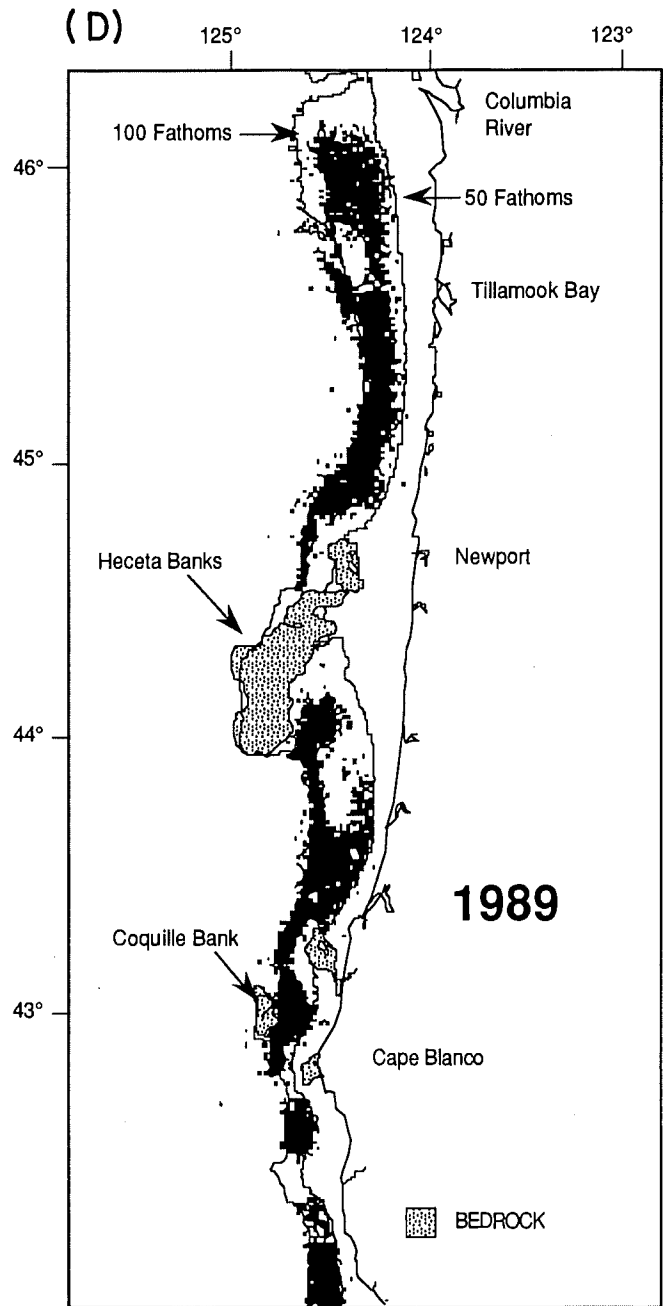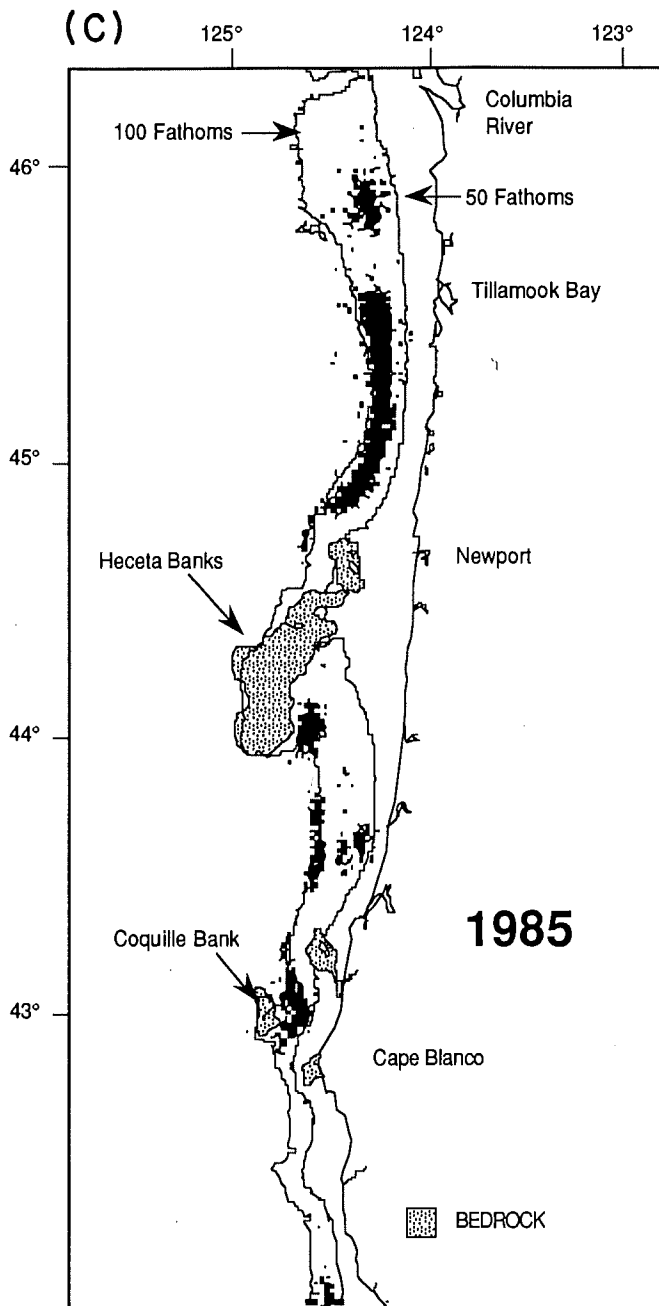
rates included hake biomass (age 2+ and age 3+), and the number of hake ages 2–7 and 3–7. These four measures of hake abundance are not independent, but rather are expected to be intercorrelated. However, they do represent different ways of measuring hake abundance, both including and excluding the newly recruited, age 2, year class. To evaluate the extent to which serial autocorrelation in the time series might be causing inflated correlations between the variables, the regression analysis was repeated on the time series after first differencing (Thompson and Page 1989).

Results

The stock area estimates obtained from commercial logbook data (Table 1, Fig. 2) show that stock area of ocean shrimp has varied slowly, but quite widely, over the 1980–1990 period. The obvious autocorrelation in this time series is encouraging; a more random pattern of variation would suggest a higher degree of error in estimating stock area. Given the wide variation in stock area, an assumption of constant catchability, at least on an interannual basis, cannot be supported for ocean shrimp. The slow change over

Fig. 5. Time series of fishing effort (single-rig equivalent h) and effort per unit stock area (single-rig equivalent h/ha) for the ocean shrimp fishery in PSMFC statistical areas 82–88, 1980–1990.

Table 2. Average monthly instantaneous total mortality rates of age 2 ocean shrimp for the months April–October, 1980–1990.

Year	Estimated mortality coefficient	R^2	F	Mean monthly fishing effort (SRE-h)
1980	0.273	0.936	73.15****	16 736
1981	0.268	0.926	30.20****	15 213
1982	0.333	0.903	46.79****	11 212
1983	0.259	0.616	8.01**	5 513
1984	0.210	0.475	4.53*	3 185
1985	0.198	0.725	13.17**	5 450
1986	0.320	0.898	43.83****	12 236
1987	0.327	0.735	13.87**	19 309
1988	0.228	0.818	22.48***	15 701
1989	0.261	0.923	59.59****	19 646
1990	0.262	0.944	83.87****	14 131

Note: Linear regression model is $\log_e(CPUE) = a + b(\text{age in months})$. Mean monthly fishing effort for the same time period each year is also shown. *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$; ****, $p < 0.005$.

time shown in Fig. 2 does suggest that catchability may be at least approximately constant within a fishing season.

A linear regression of stock area on total catch from the study area shows a strong linear relationship with positive slope (Fig. 3). This regression is highly significant ($p < 0.001$). The pattern of residuals (Fig. 3) is suggestive of slight downward curvature. The evidence of slight curvature could be due to a truly nonlinear relationship betweeen stock area and stock abundance, with area expanding less rapidly at large stock sizes. However, a simpler explanation is that total catch probably underestimates stock size when the shrimp stock is very large. Given the limitations of the approach used, the strong linear association between total catch and stock area (Fig. 3) is ample evidence that an assumption of $b = 1$ in Eq. 2 is a reasonable approximation for ocean shrimp. An examination of the maps of stock area in 1980, 1984, 1985, and 1989 (Fig. 4), in comparison with the data on total catch (Table 1) shows how stock area changed concurrently with changes in total catch. Stock area contracted from 1980–1984, with commercial concentrations of shrimp persisting in certain areas, most notably just inshore of Heceta and Coquille banks, even at very low stock size. As total catch increased from 1984–1989, the geographic range of the stock expanded outward from these areas. In 1990, catch and stock area once again declined from the levels seen in 1989.

A comparison of the time series of nominal fishing effort and fishing effort per unit stock area (Fig. 5) shows how an incorrect assumption of constant catchability can give faulty information on time trends in fishing mortality. If constant catchability is assumed, then fishing mortality is assumed proportional to fishing effort. The time series of fishing effort suggests that fishing mortality of ocean shrimp decreased from 1980–1984 and has been generally increasing since then, reaching maximum levels in the late 1980s. However, the time series of fishing effort per unit stock area shows a very different pattern, suggesting that fishing mortality is lower in recent years than in the early 1980s.

Fishing effort per unit area is also less variable than nominal effort, having a coefficient of variation of only 20.5% as compared with 45.2% for nominal effort.

Linear regressions of $\log_e(CPUE)$ for age 2 ocean shrimp versus time produced statistically significant slope estimates ($p < 0.10$) for all of the 11 years from 1980–1990 (Table 2). The estimates of average monthly total mortality ranged from a low of 0.198 in 1985 to a high of 0.333 in 1982. The regression for 1984 was only barely significant ($p < 0.10$), while all of the others showed a stronger linear relationship ($p < 0.05$ or better). The pattern of variation in $\log_e(CPUE)$ for age 2 shrimp in 1984 shows a strong decline for the months of April through August followed by a sharp increase in age 2 CPUE in September–October, which is difficult to explain. Saelens and Zirges (1985), however, in reviewing the Oregon ocean shrimp fishery in 1984, speculated that shrimp distribution was abnormal that year, possibly as a result of displacement of shrimp during the very strong 1983 El Niño event, which greatly intensified the northward flowing Davidson current.

Estimates of catchability and natural mortality for the years 1980–1990 (Table 3) show wide variation, with maximum levels of natural mortality in 1982 and 1986. The different assumed values for trawl efficiency influence both the average values of catchability and natural mortality and also the pattern of interannual variation of the estimates, although less dramatically. For example, with an asssumption of 25% trawl efficiency, the 1989 estimate of natural mortality is roughly equal to the 1980 estimate (Table 3). However, at 75% trawl efficiency, the 1989 estimate is three times higher than the 1980 estimate. Clearly, to use the approach developed here to generate accurate estimates of mean monthly natural mortality for ocean shrimp, a reasonable estimate of the average efficiency of shrimp trawls is needed.

Table 3. Estimated catchability coefficient (q) and average monthly instantaneous rate of natural mortality (M) for ocean shrimp, calculated at three assumed levels of elemental trawl efficiency, 1980–1990.

Year	25% efficiency		50% efficiency		75% efficiency	
	M	q ($\times 10^{-5}$)	M	q ($\times 10^{-5}$)	M	q ($\times 10^{-5}$)
1980	0.193	0.478	0.113	0.956	0.033	1.434
1981	0.200	0.448	0.132	0.896	0.064	1.344
1982	0.274	0.527	0.215	1.054	0.156	1.581
1983	0.205	0.971	0.152	1.942	0.098	2.914
1984	0.152	1.824	0.094	3.648	0.036	5.472
1985	0.156	0.765	0.115	1.530	0.073	2.294
1986	0.270	0.405	0.221	0.810	0.171	1.215
1987	0.253	0.385	0.178	0.770	0.104	1.155
1988	0.171	0.362	0.114	0.725	0.057	1.087
1989	0.208	0.268	0.156	0.536	0.103	0.805
1990	0.218	0.310	0.174	0.620	0.131	0.930
Mean	0.209	0.613	0.151	1.226	0.093	1.839

Table 4. Results of linear regression analysis of ocean shrimp natural mortality rates, calculated at various levels of assumed trawl efficiency, versus indices of Pacific hake abundance in U.S. waters, 1980–1990. Model is mortality rate = $a + b$(hake abundance).

Pacific hake abundance index	Intercept	Slope coefficient	Slope SE	F	R^2 (unadjusted)
25% trawl efficiency					
Biomass (millions of t)					
Age 2+		ns	—	—	—
Age 3+	—	ns	—	—	—
Numbers ($\times 10^9$)					
Sum ages 2–7	0.143	0.008**	0.003	8.646	0.490
Sum ages 3–7	—	ns	—	—	—
50% trawl efficiency					
Biomass (millions of t)					
Age 2+	0.037	0.028*	0.015	3.475	0.279
Age 3+	—	ns	—	—	—
Numbers ($\times 10^9$)					
Sum ages 2–7	0.080	0.009***	0.003	10.955	0.549
Sum ages 3–7	—	ns	—	—	—
75% trawl efficiency					
Biomass (millions of t)					
Age 2+	−0.034	0.032*	0.016	3.753	0.294
Age 3+	—	ns	—	—	—
Numbers ($\times 10^9$)					
Sum ages 2–7	0.018	0.009**	0.003	10.036	0.527
Sum ages 3–7	—	ns	—	—	—

Note: *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$; ****, $p < 0.005$; ns, nonsignificant ($p > 0.10$).

Linear regressions of shrimp natural mortality rates against age 2+ hake biomass were significant ($p < 0.10$), with assumed trawl efficiency of 50% and 75%, but nonsignificant assuming 25% trawl efficiency (Table 4). The regressions against the numbers of age 2–7 hake were significant ($p < 0.05$) for all three levels of assumed trawl efficiency. In all cases, the significant regression coefficients were positive, as expected. Both measures of the abundance of older hake, however, were nonsignificant regressors of shrimp natural mortality rates ($p > 0.10$). After first differencing (Table 5), the pattern of significant regressions is similar to the results with the raw data, with higher

Table 5. Results of linear regression analysis of ocean shrimp natural mortality rates, calculated at various levels of assumed trawl efficiency, versus indices of Pacific hake abundance after first differencing of both variables. Model is mortality rate = a + b(hake abundance).

Pacific hake abundance index	Intercept	Slope coefficient	Slope SE	F	R^2 (unadjusted)
25% trawl efficiency					
Biomass (millions of t)					
Age 2+	0.004	0.056****	0.011	24.461	0.732
Age 3+	—	ns	—	—	—
Numbers (×10⁹)					
Sum ages 2–7	0.013	0.012****	0.004	12.692	0.585
Sum ages 3–7	—	ns	—	—	—
50% trawl efficiency					
Biomass (millions of t)					
Age 2+	0.005	0.046**	0.017	7.312	0.478
Age 3+	0.006	−0.031*	0.014	4.661	0.368
Numbers (×10⁹)					
Sum ages 2–7	0.004	0.01****	0.002	21.087	0.725
Sum ages 3–7	—	ns	—	—	—
75% trawl efficiency					
Biomass (millions of t)					
Age 2+	0.004	0.026*	0.014	3.481	0.279
Age 3+	—	ns	—	—	—
Numbers (×10⁹)					
Sum ages 2–7	0.006	0.010****	0.002	17.51	0.661
Sum ages 3–7	—	ns	—	—	—

Note: *, $p < 0.10$; **, $p < 0.05$; ***, $p < 0.01$; ****, $p < 0.005$; ns, nonsignificant ($p > 0.10$).

levels of significance in some cases. This suggests that the significant regressions shown in Table 4 do not result simply from serial autocorrelation in the variables. The best linear regressions, after differencing, were between shrimp mortality rates and the numbers of age 2–7 hake ($p < 0.05$), but age 2+ biomass was also a significant regressor ($p < 0.10$). After differencing, the measures of age 3+ hake abundance were still generally nonsignificant regressors, with the exception of age 3+ hake biomass under an assumption of 50% trawl efficiency. In this case, however, the sign of the regression slope is negative and this correlation is considered spurious. Inspection of the scatterplots (not shown) and the time series graphs (Fig. 6) indicated that the significant regressions were the result of sharply increased shrimp natural mortality in 1982 and 1986, concurrent with two major hake recruitment events.

Discussion

The results of this study show that catchability and natural mortality are not constant for ocean shrimp, at least on an interannual basis. The wide variation displayed by these parameters may partly explain some of the difficulties

encountered in early attempts to model the ocean shrimp stock (Geibel and Heimann 1976) and subsequent attempts to develop a spawner–recruit relationship for this species from commercial catch and effort data (Hannah 1993). The findings of this study also support the principle conclusion of Winters and Wheeler (1985), that the assumption of constant catchability is usually violated owing to the systematic interaction between stock abundance and stock area. However, these results also suggest that in some fisheries, where stock area can be estimated, considerably more useful information can potentially be extracted from catch and effort data. For example, if variation in stock area is the main source of variation in catchability (Swain and Sinclair 1994), then fishing effort per unit area may accurately index fishing mortality for ocean shrimp (Fig. 5). Stock area data could also possibly be incorporated into other techniques, such as in constructing indices of stock and recruitment or in using fishing effort data to tune virtual population analysis. Such techniques might be best applied to fisheries which operate principally on new recruits, but for which survey information is lacking.

These results also raise some questions about previous work relating shrimp recruitment to variation in the ocean

If shrimp natural mortality rates are influenced by hake abundance, this could have important implications for future studies of ocean shrimp population dynamics. Pacific hake are seasonal migrants, abundant in the study area only from about April through October. Accordingly, shrimp natural mortality rates, which may be roughly constant within the April–October period, may decline seasonally when hake leave the study area. This could be an important factor in certain types of assessments, for example yield-per-recruit analysis.

The evidence presented here for a trophic interaction between hake and ocean shrimp, although preliminary in nature, conflicts with the conclusion of an earlier study by Livingston and Bailey (1985). They examined the available evidence and concluded that a strong argument could not be made for a major predator–prey interaction between hake and ocean shrimp. They point out, correctly, that the increase in landed catch of shrimp between 1952–1965, when hake were unexploited, and 1966–1977, when hake were being fished, was due mostly to dramatic growth in fishing effort for shrimp between the two periods. They also point out that shrimp CPUE between the two periods shows no increase, suggesting that changes in the fishing regime for hake have had no measurable impact on the abundance of shrimp. However, it's unlikely that changes in hake predation on shrimp would have caused measurable changes in mean shrimp CPUE over these time periods. First, if my earlier findings are correct (Hannah 1993), shrimp recruitment varies widely in response to environmental variation. The variation in age 2 shrimp recruitment reported for the study area is equivalent to a range of roughly 2000 – 18 000 t of shrimp (Hannah 1993). Francis (1983) calculated that the decrease in total shrimp consumption by hake between the two time periods should have ranged from about 400 to 6200 t. Accordingly, differences in average recruitment between the two time periods could easily have masked any effect on CPUE from a decrease in predator biomass. Second, shrimp show variable rates of growth that may be density dependent (Hannah and Jones 1991). They also exhibit flexible rates of sex change that are linked to the age composition of the stock, which is influenced by mortality rates (Charnov et al. 1978). Therefore, changes in the population structure of ocean shrimp, in response to changes in predation, may be visible in the age composition of the stock, but not necessarily in average CPUE. Shrimp age composition data from 1952–1965 are not available to test the hypothesis that a different shrimp age structure should be evident when hake populations were higher. However, the shift in age composition of the shrimp catch after 1978, which Hannah and Jones (1991) attributed to a fishing down process for shrimp, also coincides with the start of a period of higher hake biomass (Fig. 6). If shrimp natural mortality rates are related to hake abundance, as suggested by this study, the shift in age composition described by Hannah and Jones (1991) could be partly a result of increased hake predation, rather than simply a result of heavy shrimp fishing.

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