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Influence of Environmental Variation and Spawning Stock Levels on Recruitment of Ocean Shrimp (*Pandalus jordani*)

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The influence of environmental factors on recruitment variability in ocean shrimp (*Pandalus jordani* Rathbun) from 1967 to 1988 was investigated using correlation and multiple regression. Low sea levels during larval release in April, indicative of a strong spring transition in coastal currents, were strongly correlated with increased recruitment. Interannual changes in catch distribution showed an interaction between shrimp abundance and distribution, with reduced catches accompanying a northerly catch distribution. A linear model incorporating April sea level explained 58% of the variation in log recruitment and also correctly indicated a serious year class failure in 1989. An index of spawning stock was compared with the residuals from the linear model based on April sea level, but no stock–recruitment relationship was found.

L'auteur a étudié, par corrélation et régression multiple, l'influence de facteurs environnementaux sur la variabilité du recrutement de la crevette nordique (*Pandalus jordani* Rathbun) de 1967 à 1988. Le faible niveau de la mer pendant la période de production larvaire d'avril, qui est l'indice d'une forte transition de printemps des courants côtiers, était fortement corrélé avec l'augmentation du recrutement. Les variations interannuelles de la distribution des prises indiquaient l'existence d'une interaction entre l'abondance et la distribution des crevettes, une réduction des prises correspondant à une distribution plus vers le nord. Un modèle linéaire tenant compte du niveau de la mer en avril a permis d'expliquer 58 % de la variation du log du recrutement et indiquait, de façon exacte, l'important fléchissement de la classe de 1989. La comparaison d'un indice du stock de géniteurs avec les résidus du modèle linéaire du niveau de la mer en avril n'a pas permis de déceler de relation entre le stock et le recrutement.

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Fishable populations of ocean shrimp (*Pandalus jordani* Rathbun) are found from Queen Charlotte sound in British Columbia to California (Dahlstrom 1970). The trawl fishery for this species has exhibited large fluctuations in total catch, ranging from over 39 000 t in 1978 to only 5300 t in 1984 (PSMFC 1990). Some of this variation in catch can be attributed to fluctuations in fishing effort. The most influential factor, however, is probably variation in survival from the early larval stages to the age of recruitment. Pandalid shrimp fisheries frequently exhibit large-scale fluctuations in catch (Balsiger 1981; Clark and Anthony 1981; Gaffney 1981). These fluctuations have been attributed to a combination of changes in environmental factors effecting recruitment and rapid fishery development in response to dominant year classes (Balsiger 1981). Recruitment in other pandalid stocks and in penaeid shrimp stocks has been shown to fluctuate widely in response to changes in the environment (Dow 1964; Garcia 1983; Apollonio et al. 1986; Penn and Caputi1986; and others).

Previous research suggests that environmental variation in the northeast Pacific Ocean influences recruitment in ocean shrimp. In laboratory studies, Rothlisberg (1975) found that survival of ocean shrimp to the early larval stages declined rapidly above 11°C and that temperature tolerance widened at later larval stages. Ocean shrimp spawn in the fall each year, with females carrying the developing eggs until the following spring (Dahlstrom 1970). Larval release occurs during the months of March and April. The larvae are planktonic and are found in surface waters in the early stages, but occupy progressively greater depths as they develop. Rothlisberg (1975) suggested an early critical period for ocean shrimp during which survival could be strongly influenced by sea temperature. Rothlisberg and Miller (1983) also demonstrated a significant positive correlation between June–August upwelling on the Oregon coast and larval survival estimated from commercial landings data. Given the increased temperature tolerance of later stage larvae, and their tendency to occur at greater depth, the June–August time period is later than would be expected for a critical period based solely on sea temperature.

The 1989 year class (year of larval release unless noted) of ocean shrimp was virtually a complete failure. Catches of age 1 shrimp in the commercial trawl fishery were extremely low during the entire 1990 season, especially south of the Columbia River (Hannah and Jones 1991a). The upwelling indices used by Rothlisberg and Miller (1983) predicted recruitment for this year class to be slightly below average. The failure of the upwelling index to identify such a significant recruitment failure suggested that the relationship between ocean shrimp recruitment and the ocean environment warranted further research.

Huyer et al. (1979) demonstrated that there is a rapid "spring transition" in oceanographic conditions on the continental shelf off of Oregon each year. Winter conditions are generally dominated by northward shelf currents at all depths, winds from the south, and downwelling of coastal water. Spring–summer

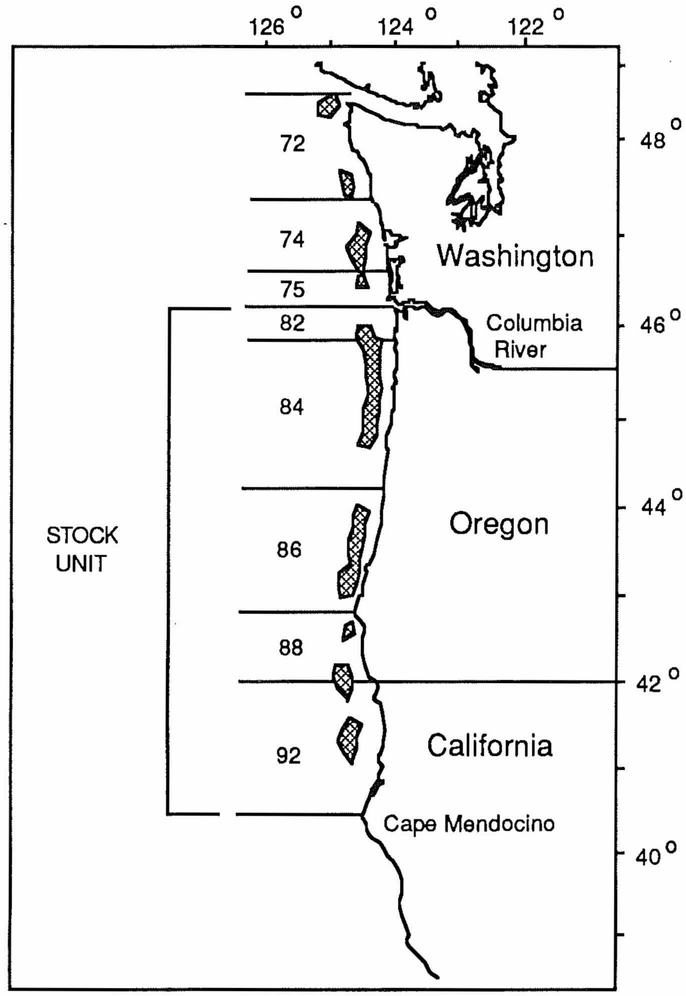

FIG. 1. Location of commercial concentrations of ocean shrimp along the U.S. Pacific coast (shaded areas) in PSMFC statistical areas 72–92.

conditions are characterized by strong southward surface currents, weak bottom currents, northwest winds, and coastal upwelling. The spring transition is most strongly reflected in coastal sea level measurements, which are generally elevated in the winter, fall rapidly in the spring, and remain depressed over the summer months (LaFond 1939; Patullo 1960; Huyer et al. 1979; Chelton et al. 1982; Hickey 1989). The timing of the spring transition coincides closely with ocean shrimp larval release. Coastal sea levels were lower than average in the winter and higher than average in the spring of 1989, suggesting a weak spring transition. The failure of the subsequent year class suggested that the intensity of the spring transition, as reflected in sea levels, may have an important influence on recruitment. The primary objective of this study was to test whether spring sea levels were correlated with ocean shrimp recruitment success.

Early attempts to develop a spawner–recruit relationship for ocean shrimp were unsuccessful (Abramson and Tomlinson 1972; Gotshall 1972). These studies, however, did not take into account the influence of variation in the environment as suggested by Garcia (1983) and others. A second objective of this study was to examine the evidence for a stock–recruitment relationship for ocean shrimp, after accounting for environmental effects.

Materials and Methods

The indices of recruitment and spawning stock used in this study were calculated from data on shrimp trawl activity for the years 1966–90. The study area extended from Cape Mendocino, California, to the Columbia River, Oregon (Fig. 1), including Pacific States Marine Fisheries Commission (PSMFC) statistical areas 82–92. The data used included total catch, fishing effort, and age and size composition of the catch for each area and month (Zirges et al. 1982; Oregon Department of Fish and Wildlife (ODFW), unpubl. data). Fishing effort was standardized for double-rigged and single-rigged trawl vessels (PFMC 1981) and expressed in single-rig equivalent hours (sre hours). For a further discussion of the data collection methods, see Hannah and Jones (1991b).

Age 2 shrimp were assumed to be fully recruited to shrimp trawl gear throughout the study area. Age 1 shrimp are incompletely recruited to the fishery (Lo 1978; ODFW, unpubl. data), especially early in the April–October fishing season. After 1978, the percentage of age 1 shrimp in the catch and mean size at age 1 increased (Hannah and Jones 1991b). A recruitment index based solely on the size of the population at age 2 would seriously underestimate recruitment after 1978. Therefore, two components were summed to calculate the index of shrimp recruitment, one based on the average catch-per-unit-effort (CPUE) for age 2 shrimp in April and May and one based on the catch of age 1 shrimp in the previous year. Each component of the index was calculated separately for each statistical area, summed across the five areas, and then combined.

The first component of the recruitment index, the average age 2 population for the April–May time period in year t, is estimated from April and May CPUE for age 2 shrimp, using the simplest form of Baranov's catch equation (Ricker 1975):

$$C/f = qN_0$$

where C = the number of age 2 shrimp caught in April and May, f = fishing effort (sre hours) in April and May, q = the catchability coefficient, and N_0 = the average age 2 population.

Prior to 1974, the fishing season for ocean shrimp in the study area opened 1 March. Afterwards, a 1 April opening date was standard. The April–May period was chosen to estimate the age 2 population because fishing effort and conditions are highly variable in March and early April, but substantial fishing effort develops by May. Using the simple sum of age 2 catch divided by the sum of effort is equivalent to an effort-weighted average of CPUE for the five areas. This approach to calculating CPUE was used to reduce the influence of increased variability in CPUE which can arise when one area receives a very low level of fishing effort. After the average age 2 population for the April–May period was calculated, the March and April catch of age 2 shrimp was added to the population estimate to generate the age 2 component of the recruitment index. This was necessary to standardize the estimates and minimize the influence of highly variable fishing effort in March and April. An estimate of q, the catchability coefficient, for area 92 was obtained from Geibel and Heimann (1976). It was assumed that q was constant at 0.0001017 and equal for each of the five areas.

The second component of the recruitment index is based on the catch of age 1 shrimp in year $t - 1$ and corrects for higher levels of harvest of age 1 shrimp after 1978. This component is calculated by discounting the monthly catch of age 1 shrimp from year $t - 1$ by an average monthly natural mortality rate for the number of months that would have elapsed until 1 April of year t. The equation for the age 1 component is

$$N_1 = \sum_{i=1}^{n} C_i e^{-TM}$$

where N_1 = the age 1 component, C_i = the catch of age 1 shrimp in year $t - 1$ and month i, n = the number of months in the shrimp season in year $t - 1$, T = the number of months between month i and 1 April of year t, and M = the average instantaneous monthly rate of natural mortality.

The age 1 component actually represents a crude estimate of the number of additional age 2 shrimp that would have been present on 1 April of year t, if there had been no harvest of age 1 shrimp in year $t - 1$. The monthly rate of natural mortality used for discounting the age 1 catches was 0.096, obtained from Gotshall (1972). In employing this rate as a constant, it was assumed that there had been no time trends in natural mortality across the 1966–90 period. While this may be a reasonable assumption, monthly natural mortality rates are probably quite variable, and using a constant value injects an unknown level of additional variance into the recruitment index. Consequently, after 1976, when age 1 catch levels are higher, this index may be a less accurate measure of recruitment. Estimates of monthly or annual natural mortality rates are not available to correct for this problem.

A simple mean of the CPUE values (kilograms per sre hour) for all five areas, for the months of September and October, was used as an index of the ocean shrimp spawning stock. Since 1978, when shrimp size at 1 increased, age 1 shrimp have been fully recruited to trawl gear by September. In some of the early years of the fishery, especially when shrimp growth was poor, age 1 shrimp were probably not fully recruited to trawl gear by September (Lo 1978; ODFW, unpubl. data). Accordingly, the spawning stock index used in this study may understate the actual spawning biomass in some of the early years of the time series. However, this may still be the best index of the shrimp spawning stock available. Ocean shrimp are protandric hermaphrodites. They have been shown to exhibit very flexible rates of sex change in response to fluctuations in age class structure (Charnov et al. 1978) and show evidence of density-dependent growth (Hannah and Jones 1991b). These findings suggest that the breeding population is likely to remain roughly balanced between males and females (Hannah and Jones 1991b) and show increased age-specific fecundity when growth is increased. Since data are not available to estimate annual age-specific fecundity, late-season biomass, if reflected accurately in changes in CPUE, is probably the best measure of egg production available.

One important difficulty in using CPUE as a proxy for abundance or biomass in ocean shrimp (i.e. assuming a constant q) is the effect of gear development and improvements in fleet efficiency from 1966 to the present (Hannah and Jones 1991b). The data on fishing effort employed in this study are corrected for the difference in efficiency between single-rigged and double-rigged vessels (one double-rigged hour is equivalent to 1.6 sre hours) but not explicitly for other changes in efficiency. These include the gradual increase in average vessel size over time, the switch in the late 1970's to high rise nets (Zirges and Robinson 1980; Hannah and Jones 1991b), and the development of sophisticated electronics for trawl vessels. There are several reasons why the bias introduced by these factors may be small enough to ignore. First, the time period during which the shrimp fleet was slowly converting from mostly single-rigged to mostly double-rigged vessels, 1974–80, is the same time period during which average vessel size increased, high rise nets became prevalent, and many of the advances in vessel electronics came into widespread use. In effect, the various improvements in fishing technology are confounded and may already be substantially accounted for in the single-rig to double-rig conversion factor. Second, there is evidence of gear interference at high effort levels (D. R. Bernard, Oregon State University, Corvallis, OR, 1983 draft), which would act to offset improvements in gear efficiency for many recent years. Gear interference in this fishery could arise from physical competition for space on the limited trawlable ground. A more likely source of interference could arise from the fleet spending more time fishing on less dense aggregations of shrimp than in the early years of the fishery, due to the stock being reduced from virgin levels. Finally, any bias that might be introduced to the recruitment index would be reduced after 1978 by the increased contribution of the age 1 component, which is not dependent on CPUE.

Although the primary objective of this study was to test whether spring sea levels were routinely related to recruitment success, a broad set of environmental measures from the pelagic larval time period were examined. The time period considered was limited to 10 mo after larval release, as it was assumed, a priori, that early larval or juvenile effects probably determined year class strength. The independent variables selected for analysis included sea level at Crescent City, California, sea surface temperature (SST) at 43°N, 125°W, and the coastal upwelling index at 45°N. The Crescent City sea level series was selected over other areas because it is close to the study area and has a very complete time series. For all of the variables, mean values from 2-mo time periods were used, beginning in March of the year of larval release and continuing through the following February. The environmental data were obtained from several sources. Sea level height data were provided by the National Oceanic and Atmospheric Administration (NOAA) archives, through the Sea and Lake Levels Branch. SST data originated from NOAA's Comprehensive Ocean-Atmosphere Data Set (COADS) described by Woodruff et al. (1987). Both the COADS temperatures and recent values for the upwelling index were obtained through the National Marine Fisheries Service's Pacific Marine Environmental Laboratory. The upwelling index for the years prior to 1973 came from Bakun (1973).

A stepwise process was used to analyze the relationship between the environmental variables and the shrimp recruitment index. First, scattergrams of each relationship were inspected for evidence of curvilinearity or heteroscedasticity. A number of the scattergrams indicated both effects, so the recruitment index was transformed using the natural logarithm (Ricker 1975). The evidence of log-linear relationships is not surprising, since minor changes in factors such as temperature or sea level can correspond to large-scale effects on the ocean environment. Correlation analysis was then used to assess the relationships between the environmental variables and the transformed recruitment index. The problem of serial autocorrelation within the individual time series was addressed using the method employed by Kope and Botsford (1990). This method results in an adjusted variance for the correlation coefficient, r, based on the autocorrelation functions of the two variables.

Initial results suggested that the 1982 data point was a clear

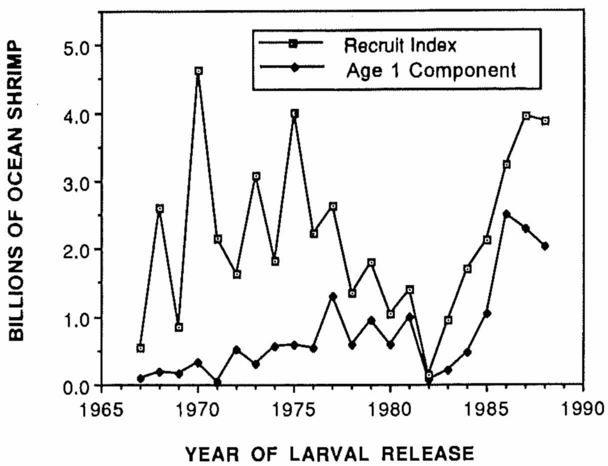

FIG. 2. Ocean shrimp recruitment index, and the age 1 component of the index, by year of larval release, 1967–88.

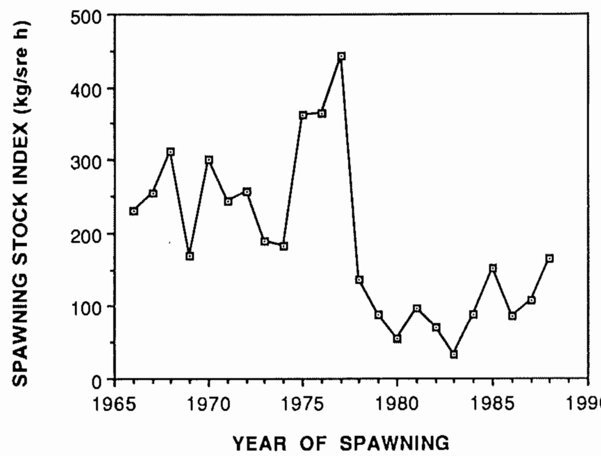

FIG. 3. Ocean shrimp spawning stock index (kg/single-rig equivalent h), 1966–88.

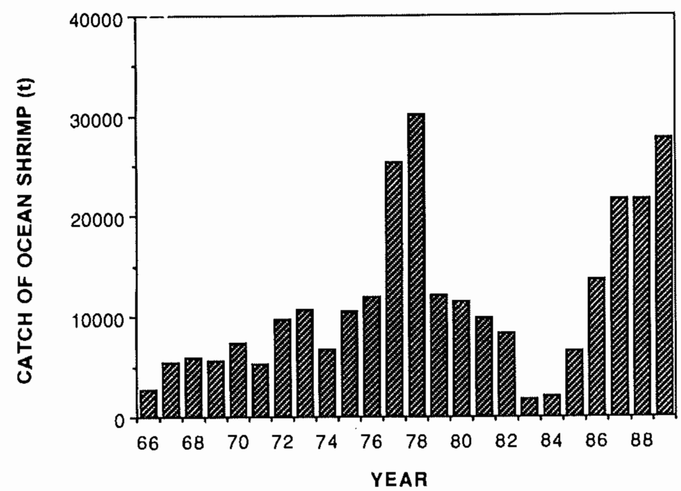

FIG. 4. Total catch of ocean shrimp from the study area, 1966–89.

outlier in many of the univariate correlations. Larvae released in 1982 developed during the 1982–83 El Niño event, which had extreme effects on fish stocks and zooplankton assemblages of the North Pacific Ocean (Miller et al. 1985; Pearcy et al. 1985). The primary interest of this investigation was in the more routine influence of the environment on shrimp recruitment, not the effect of extreme events. Accordingly, the univariate correlations were also calculated with the 1982 data point deleted. Next, linear regression was used to investigate, in more detail, the relationship between monthly mean sea level and $\log_e$ recruitment, for selected months. In this, and all subsequent analyses, the 1982 data point was excluded, and no correction for serial autocorrelation was used. Stepwise regression was then used to determine whether a combination of environmental factors could explain a major portion of the variation in the transformed recruitment index. Although no correction for serial autocorrelation was used in this analysis, variables were entered or removed from the stepwise regression at a significance level of $p < 0.01$ rather than $p < 0.05$ to prevent variables with weak explanatory power from entering the terminal model.

Walters and Collie (1988) have suggested that studies of fish–environment interactions have generally been more successful at demonstrating changes in distribution than changes in survival. There is abundant evidence that the environmental factors being examined here are closely tied with the strength of alongshore coastal currents (Reid and Mantyla 1976; Huyer and Smith 1985; Hickey 1989). Coastal currents are more coherent from surface to bottom in winter than in other seasons and could shift the geographical distribution of the adult population of shrimp, giving the appearance of an effect on recruitment (Huyer et al. 1979; Hickey 1989). Saelens and Zirges (1985) speculated that the 1982–83 El Niño event may have intensified the northward flowing Davidson current and shifted the entire stock northward for 1983. Although most work has focused on the onshore–offshore transport effects of upwelling, the magnitude of alongshore surface transport in the spring is likely to exceed the onshore–offshore component (Hickey 1989). To evaluate whether any apparent environmental effects on recruitment were really only influencing distribution, I also examined interannual changes in the percentage of the ocean shrimp catch taken inside the study area and from areas further north.

The residuals from the best environmental model were tested for evidence of a stock–recruitment relationship using a stepwise process. First, average values of the environmental variables were substituted into the model to calculate $\log_e$ recruitment under average environmental conditions. This value was then added to the model residuals and the resulting data series was back-transformed. This process provides a series of recruitment index values that are "adjusted" to average environmental conditions. The graph of these adjusted values versus the spawning stock index was inspected graphically for evidence of a stock–recruitment relationship and to determine the approximate form of the function. Garcia (1983) has suggested that many apparent stock–recruitment relationships in shrimp stocks are artifacts arising from serial autocorrelation within the recruitment indices of short-lived stocks. The adjusted recruitment index values were examined for evidence of correlation at a lag of 1 yr to address this concern. Multiple linear regression was then used to test the fit of a composite model incorporating the apparent stock–recruitment function.

Results

The ocean shrimp recruitment index (Fig. 2) shows wide fluctuations from 1967 to 1988 but no evidence of a sustained decline. The index of spawning stock biomass (Fig. 3) is generally decreased after 1977, due to some years of low recruitment

TABLE 1. Linear correlations between the natural logarithm of the ocean shrimp recruitment index and selected environmental variables. Coefficients significant at the 0.05 level using simple correlatin methods are shown. Asterisks depict levels of significance after correction for serial autocorrelation within a series (*$p < 0.05$; **$p < 0.01$).

Variable	Time period	Months after larval release	Correlation coefficient
Sea surface temperature	Mar.–Apr.	0	ns
	May–June	2	ns
	July–Aug.	4	ns
	Sept.–Oct.	6	−0.490
	Nov.–Dec.	8	ns
	Jan.–Feb.	10	−0.537*
Upwelling index	Mar.–Apr.	0	ns
	May–June	2	−0.469*
	July–Aug.	4	ns
	Sept.–Oct.	6	0.439
	Nov.–Dec.	8	ns
	Jan.–Feb.	10	0.688**
Sea level height	Mar.–Apr.	0	−0.648**
	May–June	2	ns
	July–Aug.	4	ns
	Sept.–Oct.	6	−0.577*
	Nov.–Dec.	8	ns
	Jan.–Feb.	10	−0.597*

TABLE 2. Crosscorrelations of mean sea level (SL) at Crescent City, California, mean sea surface temperature (SST) at 43°N, 125°W, and the mean upwelling index (U) at 45°N, 125°W for selected 2-mo intervals for 1967–88. Asterisks depict standard levels of significance without correction for serial autocorrelation between years (*$p < 0.05$; **$p < 0.01$).

Variable	Months after larval release	Mar.–Apr. SL	Sept.–Oct. SL	Jan.–Feb. SL	Jan.–Feb. SST	May–June *U*	Jan.–Feb. U
Mar.–Apr. SL	0	1.000					
Sept.–Oct. SL	8	0.552**	1.000				
Jan.–Feb. SL	10	0.127	0.617**	1.000			
Jan.–Feb. SST	10	0.158	0.695**	0.642**	1.000		
May–June U	2	0.316	0.211	0.451*	0.138	1.000	
Jan.–Feb. U	10	−0.235	−0.496*	−0.793**	−0.738**	−0.420	1.000

and several years of high catch (Fig. 4). Although not shown, the graph of the recruitment index versus the parent year spawning biomass index showed no discernible relationship. This suggests that either environmental effects have been the primary influence on recruitment over the years in question or errors in the indices are obscuring any relationship.

The correlation analysis (Table 1) shows several significant linear correlations ($p < 0.05$) between the environmental variables tested and $\log_e$ of the recruitment index. Sea level and SST are consistently negatively correlated with shrimp recruitment. The upwelling index shows both positive and negative correlations with recruitment, suggesting a more complex relationship or spurious correlations. Six of the 18 comparisons are significant, even after correction for serial autocorrelation. Only one significant correlation in 20 would be expected by chance alone. The correction for serial autocorrelation reduced the significance level for several of the correlations. The high number of significant correlations is partially explained by crosscorrelation between the variables (Table 2). The upwelling index, sea level, and SST are well correlated in January–February. Many of the other variables show some degree of crosscorrelation as well. The six significant correlations clearly represent a much smaller number of real environmental effects on shrimp recruitment.

Scattergrams of several of the significant environmental variables (Fig. 5–8) show that for many of the variables, the 1982 data point is an outlier. The low recruitment to the study area for this year class may have resulted from the stock being shifted northward in the winter of 1983 (calendar year) rather than from effects on shrimp survival (Saelens and Zirges 1985). With 1982 excluded (Table 3), March–April sea level shows by far the strongest correlation with shrimp recruitment ($p < 0.01$). The variables related to winter ocean conditions 10 mo after larval release, which show good correlations with $\log_e$ shrimp recruitment in Table 1, all show reduced correlation coefficients in Table 3. May–June sea level and September–Otober SST and sea level are also correlated with recruitment success ($p < 0.05$), but less strongly than March–April

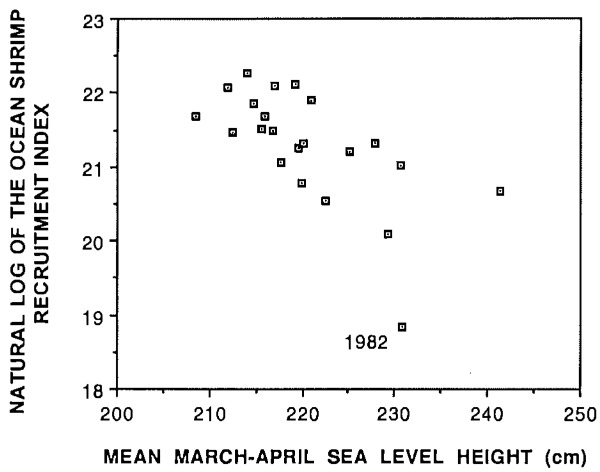

FIG. 5. Natural logarithm of the ocean shrimp recruitment index versus mean sea level at Crescent City, California, during March–April of the year of larval release. Data shown are for spring larval release, 1967–88.

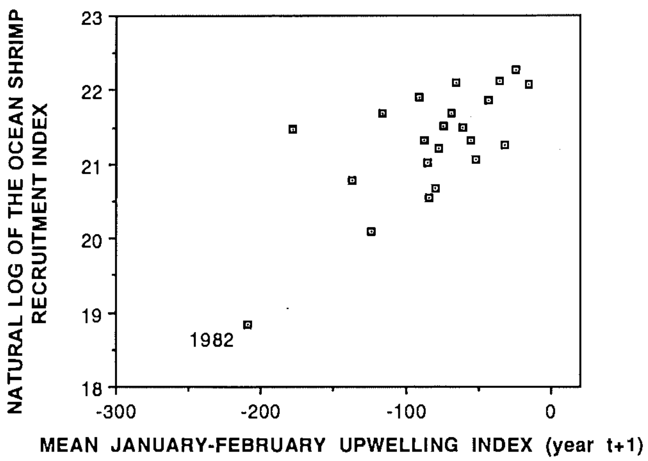

FIG. 6. Natural logarithm of the ocean shrimp recruitment index versus the mean upwelling index at 45°N, 125°W during January–February of the year following larval release. Data shown are for spring larval release, 1967–88.

sea level. Due to the data gap created by deleting the 1982 data point, the comparisons in Table 3 are not corrected for serial autocorrelation. This leaves some doubt as to whether some of the marginally significant correlations would remain so after such correction.

Linear regressions of $\log_e$ recruitment versus mean sea level for March and April show that April sea level is a better single predictor of shrimp recruitment than either March sea level or the March–April mean (Fig. 9 and 10; Table 3). April sea level alone explains 58% of the variation in $\log_e$ recruitment ($p < 0.005$), while the regression with March sea level is nonsignificant. Stepwise regression analysis on all of the variables results in a simple linear regression model based on April sea level, suggesting that the other environmental variables do not explain a significant degree of residual variation in shrimp recruitment ($p > 0.01$). Fitted values (back-transformed) from this model mirror most of the major fluctuations in the recruitment index from 1967 to 1988 (Fig. 11). The fact that the model incorporates March–April sea level with a negative sign, as was suspected a priori, is encouraging. The model also predicts a

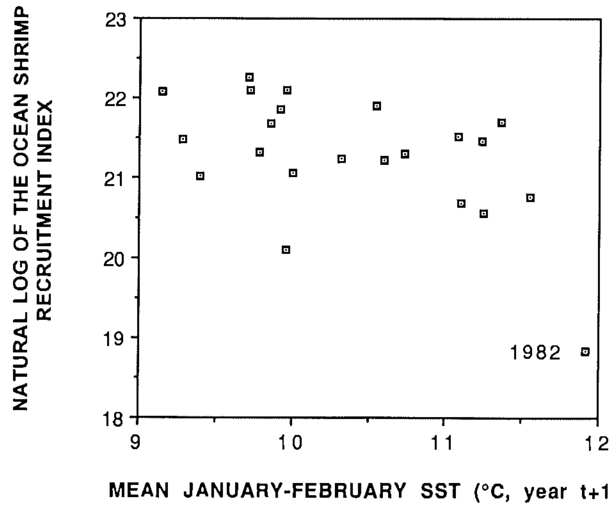

FIG. 7. Natural logarithm of the ocean shrimp recruitment index versus mean SST at 43°N,125°W during January–February of the year following larval release. Data shown are for spring larval release, 1967–88.

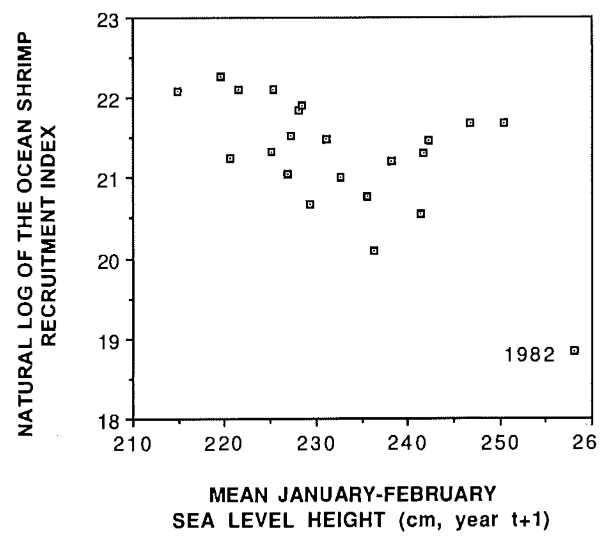

FIG. 8. Naural logarithm of the ocean shrimp recruitment index versus mean sea level at Crescent City, California, during January–February of the year following larval release. Data shown are for spring larval release, 1967–88.

recruitment level of 1.3 billion shrimp for the failed 1989 year class. This would be well below average for the 21-yr time series and lie within the bottom 25% of observed recruitment values.

These data provide evidence that sea level at the time of larval release exerts a strong and routine effect on subsequent shrimp recruitment to the study area. One alternative hypothesis worth examining is that April sea level primarily influences shrimp distribution. The drop in spring sea level is associated with the intensification of southward surface flow (Huyer et al. 1979), which could simply carry more larvae into the study area. If such shifts in distribution are the dominant mechanism by which the shrimp population within the study area is determined, then we should see a tendency for high catches within the study area to be associated with reduced catches to the north. This effect should be especially strong when we compare catch

TABLE 3. Linear correlations between the natural logarithm of the ocean shrimp recruitment index and selected environmental variables, with the 1982 data point deleted. Coefficients significant at the 0.05 level using simple correlation methods are shown. Asterisks depict standard levels of significance without correction for serial autocorrelation (* $p < 0.05$; ** $p < 0.01$).

Variable	Time period	Months after larval release	Correlation coefficient
Sea surface temperature	Mar.–Apr.	0	ns
	May–June	2	ns
	July–Aug.	4	ns
	Sept.–Oct.	6	−0.457*
	Nov.–Dec.	8	ns
	Jan.–Feb.	10	ns
Upwelling index	Mar.–Apr.	0	ns
	May–June	2	ns
	July–Aug.	4	ns
	Sept.–Oct.	6	ns
	Nov.–Dec.	8	ns
	Jan.–Feb.	10	0.473*
Sea level height	Mar.–Apr.	0	−0.645**
	May–June	2	−0.471*
	July–Aug.	4	ns
	Sept.–Oct.	6	−0.497*
	Nov.–Dec.	8	ns
	Jan.–Feb.	10	ns

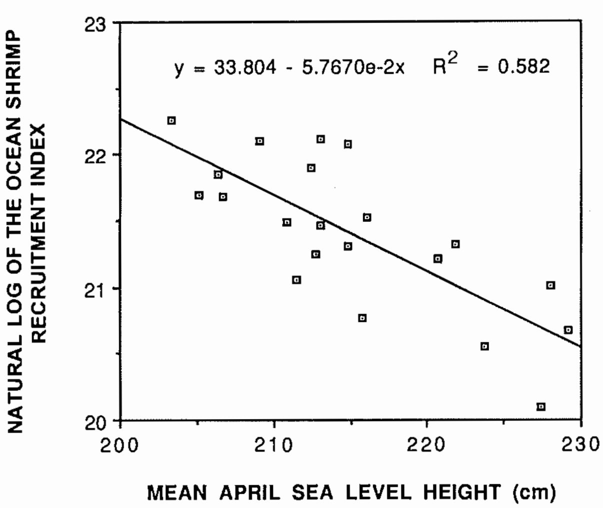

FIG. 9. Linear regression of the natural logarithm of the ocean shrimp recruitment index versus mean sea level at Crescent City, California, in April of the year of larval release. Data shown are for spring larval release, 1967–88, excluding 1982.

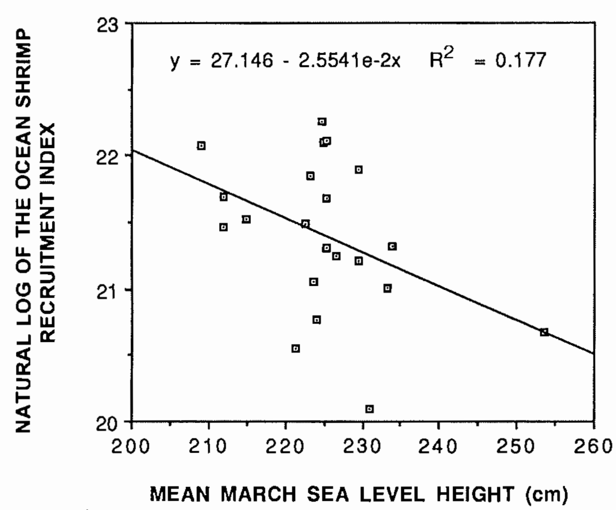

FIG. 10. Linear regression of the natural logarithm of the ocean shrimp recruitment index versus mean sea level at Crescent City, California, in March of the year of larval release. Data shown are for spring larval release, 1967–88, excluding 1982.

in the study area with catch in British Columbia, the northern limit of commercial concentrations of *P. jordani*.

The data on interannual changes in catch distribution suggest a link between effects on shrimp distribution and shrimp abundance. Table 4 shows the total catch of pandalid shrimp for the study area and from waters off Washington and British Columbia (PSMFC area 66 only) for 1979–89 (year of catch). Prior to 1979, the distribution of catch is probably not a good indicator of the distribution of recruits, since the catch was still dominated by age 2 and 3 shrimp (Hannah and Jones 1991b). Afterwards, age 1 shrimp dominated the catch from the study area. For these areas, the total pandalid catch is dominated by *P. jordani* (Butler 1980). Also shown is the percentage of the total catch from north of the Washington–Oregon border. This table provides evidence for a northward shift of the stock in 1983, but shows a much stronger tendency for catches to be positively correlated along the coast. Catch north of the Washington–Oregon border shows a significant positive correlation ($p < 0.01$) with both catch to the south and the shrimp recruitment index for the same catch year ($p < 0.05$). Catch from the study area is also positively correlated with catch from British Columbia ($p < 0.01$). The table also shows a tendency for large total catch to be associated with a more southerly catch distribution, and reduced catch with a northerly distribution, an

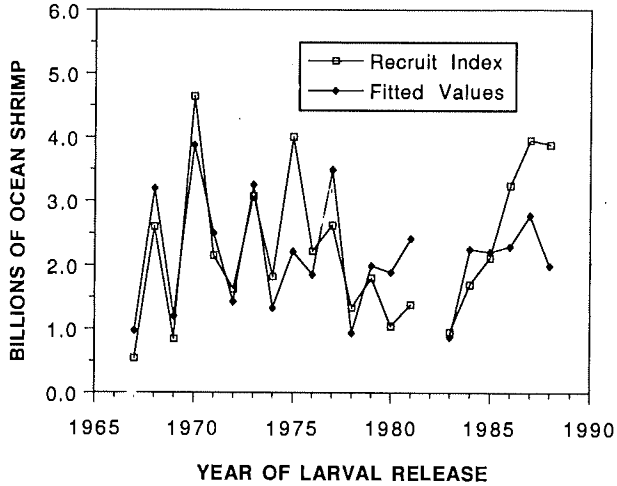

FIG. 11. Ocean shrimp recruitment index versus predicted values (back-transformed) from the environmental model based on April sea level for larval release years 1967–88.

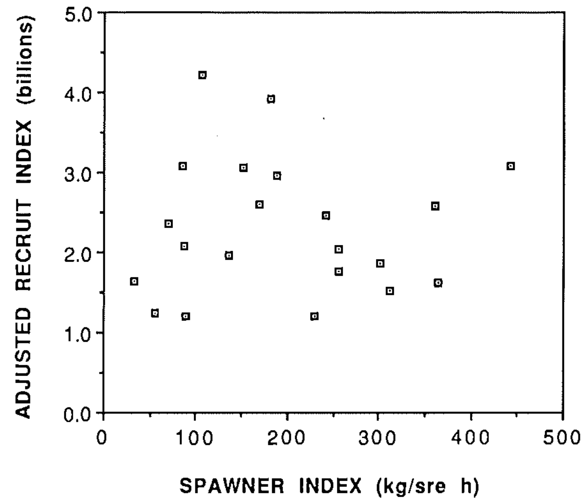

FIG. 12. Ocean shrimp recruitment index, adjusted for environmental effects, versus the spawning stock index from the parent year.

TABLE 4. Landings (t) of pandalid shrimp, primarily *P. jordani*, from the study area (Oregon and northern California) and from waters off of Washington and British Columbia[a], 1979–89. Percentage of total landings from north of the Washington–Oregon border is also shown.

Year	British Columbia	Washington	Study area	Total	Northern percentage
1979	235	8573	12104	20912	42.1
1980	136	9099	11467	20702	44.6
1981	403	7730	9923	18056	45.0
1982	183	4197	8231	12611	34.7
1983	40	3910	1702	5652	69.9
1984	41	2180	2144	4365	50.9
1985	382	5909	6843	12774	49.3
1986	1057	12056	13662	26775	49.0
1987	2535	8644	21718	32897	34.0
1988	2223	10161	21670	34054	36.4
1989	2169	7824	27738	37730	26.5

[a]British Columbia landings are from PSMFC area 66 only.

indication of interaction between factors influencing abundance and distribution of recruits.

A closer examination of the effects of the 1982–83 El Niño event on shrimp catch distribution suggests that winter ocean conditions may be having more of an effect on shrimp distribution, while spring sea levels are more directly influencing survival. This ENSO event caused a very strongly negative January–February upwelling index and elevated March–April sea levels in calendar year 1983, which should have influenced recruitment of the 1982 and 1983 year classes, respectively. The catch distribution for 1983 (1982 year class), presumably influenced by winter ocean conditions in 1983, shows a definite northward shift (Table 4), while the catch distribution for 1984 does not. However, catch in 1984 is even lower than in 1983. Of course, interannual changes in the distribution of catch could result from differential survival, rather than a wholesale shifting of the stock northward.

The recruitment index, after adjustment for the effects of April sea level, is shown versus the spawning stock index in Fig. 12. The scattergram shows, if anything, a vague suggestion of a domed (Ricker type) stock–recruitment relationship. The adjusted recruitment index shows no evidence of significant autocorrelation at a lag of 1 yr ($p > 0.05$), which would complicate testing for a statistically significant stock–recruitment relationship. The results of fitting a composite model incorporating the Ricker stock–recruitment relationship is shown in Table 5. The low partial F-values for the stock–recruitment terms suggest that changes in spawning stock do not explain a useful degree of the residual variation in shrimp recruitment after accounting for environmental variation.

Discussion

The analysis presented here shows that internannual variation in sea level at the time of larval release correlates well with variation in ocean shrimp recruitment. This connection between recruitment in ocean shrimp and the ocean environment is not a new idea. However, these results suggest different mechanisms by which the environment may be influencing recruitment. It has been argued by Rothlisberg and Miller (1983) that surface water temperatures during the larval phase may directly impact survival. Rothlisberg (1975) demonstrated that temperature has a strong influence on survival of ocean shrimp larvae in the laboratory. This study showed that the spring drop in sea level influences recruitment but did not identify spring or early summer SST as important. Early spring

TABLE 5. Results of fitting a composite model incorporating the Ricker stock–recruitment function, using multiple linear regression. Data are for larval release years 1967–88, excluding 1982. Model is $\log_e$ (recruit index) = $a + b_1(\log_e$ (spawner index)) + b_2(spawner index) + b_3(April sea level). ***$p <$ 0.005.

Parameter	Coefficient	95% confidence interval Lower	95% confidence interval Upper	Partial F-value	R^2 (adjusted)
a	31.745				
b_1	0.426	−0.0418	1.271	1.133 ns	
b_2	−0.002	−0.007	0.003	0.899 ns	
b_3	−0.056	−0.031	−0.076	23.059***	
Full model					0.537

SST's are generally within the range of 8–11°C found to be favorable for early larval survival (Rothlisberg 1975; Hickey 1989) and are higher, and consequently more critical to larvae, later in the year. Since larvae occupy greater depths as they develop and show a wider temperature tolerance as well, it is unlikely that water temperature directly limits shrimp survival except in very warm years, or in combination with reduced salinity (Rothlisberg 1975).

Several authors have argued that very strong spring upwelling may be detrimental to recruitment in species with planktonic larval forms by causing excessive offshore transport of larvae (Parrish et al. 1981). This study provides very little evidence to support this hypothesis for ocean shrimp. Figure 9 shows no evidence that $\log_e$ recruitment declines at very low spring sea levels, which would be evidence of an adverse impact caused by an excessively strong spring transition. The existence of subsurface onshore return flows (Hickey 1989) and the fact that larvae occupy deeper water as they develop argue that onshore–offshore larval transport may be quite complex.

It has also been suggested that the onset of spring upwelling transports cold, nutrient-rich water to the surface, favoring the development of larval food sources (Rothlisberg and Miller 1983). The results of this study are consistent with this hypothesis, even though the March–April upwelling index does not correlate directly with recruitment. The work of Huyer et al. (1979), describing the spring transition in detail for 1973 and 1975, suggests that the spring transition is triggered by southward wind of sufficient duration to produce a critical level of cumulative offshore Ekman transport. It follows that the drop in sea level in March–April is a more direct indicator of the onset of the upwelling season than the mean March–April upwelling index. The upwelling index is an estimate of wind-driven offshore Ekman transport which, on a mean monthly basis, may not reliably indicate whether an event of critical intensity and duration has occurred.

The data on interannual changes in the north–south distribution of catch suggest that changes in ocean shrimp abundance are positively correlated over a wide area of the Pacific coast. Northerly shifts in catch distribution also coincide with low total stock size, while increased stock size is associated with a more southerly distribution, suggesting a complex interaction between distribution and abundance. Although previous hypotheses have emphasized the importance of nutrients, this interaction suggests another hypothesis for how the timing of the spring transition could be influencing shrimp larval survival. With an early spring transition, initial larval transport should be southward and offshore and northward and onshore for a delayed transition. The onshore transport that precedes a late spring transition could carry larvae into very nearshore waters and into the surf zone, where poor survival would be expected. The fact that weak year classes fair better in the northern part of the stock range could be because the shrimp grounds are farther offshore, due to a wider continental shelf (Hickey 1989). Accordingly, it would take a longer period of onshore transport to have the same detrimental effect on recruitment in the northern area. There are, of course, other differences in the ocean environment north and south of the Washington–Oregon border, such as temperature and the seasonal influence of the Columbia River plume, which could also be causing the observed differences in how a late spring transition affects recruitment. A thorough study of how environmental factors correlate with shrimp recruitment success off the Washington coast may help explain this interaction between shrimp catch distribution and recruitment success.

This study provides virtually no evidence for a meaningful stock–recruitment relationship for ocean shrimp. This is not surprising, since stock–recruitment functions are very difficult to detect in stocks with high and variable rates of natural mortality (Koslow 1992) and in stocks with environmentally driven recruitment (Goodyear and Christensen 1984). Penn and Caputi (1986) fit a Ricker-type curve to spawning stock and recruitment data for the tiger prawn (*Penaeus esculentes*) but presented little evidence in support of the selection of any particular recruitment function. It has been assumed that, for penaeid shrimp stocks, the asymptotic curve of Beverton and Holt (1957) is appropriate (Neal 1975; Garcia 1983). This assumption is based on the concept that estuarine nursery areas utilized by penaeids may have a relatively constant carrying capacity. This line of reasoning is invalid for ocean shrimp which do not utilize estuaries. The most appropriate form of recruitment curves for pandalid shrimp remains an open question.

The hazards of correlative studies of recruitment and environmental effects have been discussed thoroughly by a variety of authors (Shepherd et al. 1984; Sissenwine 1984; Walters 1985; Walters and Collie 1988; and others). This study corrects for serial autocorrelation and attempts to adjust for some of the other pitfalls of exploratory correlation analysis. Even so, the residuals from the best environmental model are sufficiently large as to render it of limited utility for predicting shrimp recruitment. Even if further development does yield an adequate prediction equation for shrimp recruitment, it is difficult to see how this would be useful for management of the stock (Walters and Collie 1988).

Correlative studies do serve useful purposes, however, and may be especially important for shrimp stocks. It is generally accepted that recruitment in shrimp stocks is primarily environmentally driven, while stock–recruitment relationships have only rarely been demonstrated (Garcia 1983). Research on environmental factors can help to develop hypotheses about the mechanisms by which the environment determines recruitment levels, which can then be further tested using more specific approaches. Ocean shrimp, in particular, exhibit a life history that seems resistant to over-harvest (Hannah and Jones 1991b). The fact that environmental factors have substantial influence in determining recruitment success further argues that fishing is not depressing recruitment. However, to ignore the potential effect of fishing on parent stock levels defies the common sense notion that some underlying relationship between parent stock and recruitment must exist. Shepherd (1982) has stressed that the most fundamental aspect of a stock–recruitment relationship is that zero parent stock provides for zero recruitment and that fisheries do collapse. This study supports the contention of Garcia (1983), and others, that a thorough understanding of the environmental mechanisms which influence shrimp recruitment must be gained before meaningful information on how fishing influences recruitment will emerge.

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