

**Abstract.**—Using improved indices of age-1 recruitment and parent stock, I investigated the existence of a stock-recruitment relationship for ocean shrimp, *Pandalus jordani*. I also examined the effects of large catches of egg-bearing shrimp in April on subsequent recruitment. After known environmental influences were accounted for, regression analysis revealed evidence of a quasilinear relationship between recruitment and either spawning stock or egg production. The stock-recruitment relationship showed that average recruitment increases if higher spawner abundance is maintained in years of low abundance. The recruitment-stock relationship, however, showed that low abundance of spawning fish was mostly a result of environmentally driven recruitment failures, rather than just fishery impacts. Fishing did contribute to the low numbers of spawning fish in 1993, and catches of egg-bearing shrimp in April 1989 may have also depressed the 1990 year class. The strong recruitment-stock relationship for ocean shrimp suggests that an increase in escapement of all ages of shrimp in response to a year-class failure may do more to bolster recruitment than traditional strategies aimed at protecting age-1 shrimp.

## A new method for indexing spawning stock and recruitment in ocean shrimp, *Pandalus jordani*, and preliminary evidence for a stock-recruitment relationship

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Recruitment of the ocean shrimp, *Pandalus jordani*, to the fishery in waters off Oregon has been shown to be influenced strongly by ocean conditions during early larval stages (Hannah, 1993). Specifically, sea level height (SLH) during the month of April, shortly after the bulk of larval release, is strongly negatively correlated with recruitment of age-1 shrimp to the fishery the following year (Hannah, 1993). Although the mechanism linking recruitment to April SLH remains unclear, April SLH probably integrates the strength and timing of the spring transition in coastal currents (Huyer et al., 1979). Ocean shrimp larvae inhabit the near-surface waters shortly after release, occupying progressively deeper strata as they develop (Rothlisberg, 1975; Rothlisberg and Miller, 1983). The nature of the spring transition probably influences the alongshore transport of early larvae, as well as the nearshore temperature regime, either of which could strongly influence shrimp larval survival (Rothlisberg, 1975; Rothlisberg and Miller, 1983; Hannah, 1993; McConnaughey et al., 1994).

Attempts to relate ocean shrimp recruitment to the size of the parent spawning stock, even allowing for the influence of April SLH, have been unsuccessful (Abramson and

Tomlinson, 1972; Gotshall, 1972; Geibel and Heimann, 1976; Hannah, 1993). Efforts to date have, to a large degree, relied on assumptions of constant catchability and natural mortality. Recently, both natural mortality rates and the catchability coefficient have been shown to be quite variable for ocean shrimp (Hannah, 1995). I have suggested previously that variation in catchability and natural mortality may have created large enough errors in prior indices of shrimp stock and recruitment as to obscure an underlying relationship between these two variables (Hannah, 1995). In the present study, new indices of ocean shrimp recruitment and spawning stock were developed which do not rely, or rely only very minimally, on assumptions of constant catchability and natural mortality. The main objective of this study was to re-examine the relationship between shrimp recruitment and both shrimp spawning stock and April SLH in the year of larval release, using these improved indices.

Another problem with earlier studies of ocean shrimp stock size and recruitment is that they have relied on measures of parent stock or spawning biomass, rather than on more direct measures of reproductive output, such as estimates of

egg production (Rothschild and Fogarty, 1989; Hannah et al., 1995). A second objective of this study was to construct, in addition to an improved index of spawning stock, an index of egg production, and evaluate the relationship between recruitment and egg production. One of several challenges in constructing such an index is that the trawl fishery harvests egg-bearing female shrimp in late October, just before the fishing season ends, and again in early April, as fishing resumes. It can be argued that because of reduced fishing effort late in the season in most years and because of the high natural mortality rates experienced by ocean shrimp over the winter, the harvest of egg-bearing shrimp in October should have a negligible impact on total larval release the next spring. However, in April, when larval release is imminent for any shrimp still bearing eggs, the impact of the fishery could be more detrimental. Also, with much of the larval release taking place before the fishing season opens on 1 April, fishery impacts are concentrated on late-release larvae. If, as postulated in the prior study (Hannah, 1993), the timing of the spring transition is critical to larval survival or retention in the study area, the fishery may be impacting the larvae with the greatest chances for success in a poor environment: those destined for release after a late spring transition. A third objective of this study was to estimate the harvest of egg-bearing shrimp in April and examine the impact that April harvest of egg-bearing shrimp may have had on subsequent recruitment.

## Materials and methods

In my earlier study of ocean shrimp stock and recruitment (Hannah, 1993), I used an age-structured index of recruitment calculated by summing two components. The first component was an estimate of the age-2 shrimp population in April (year  $t$ ), calculated from the average fishery catch per unit of effort (CPUE) of age-2 shrimp in April and May, divided by an assumed catchability coefficient calculated from data in Geibel and Heimann (1976). The second component was simply a sum of the catch of age-1 shrimp during the prior year ( $t-1$ ), with each monthly catch discounted to 1 April of year  $t$  by using an assumed monthly natural mortality rate of 0.096 (Gotshall, 1972). In essence, this index was a crude estimate of what the age-2 shrimp population would have been in the absence of fishing, on 1 April of the age-2 year (Hannah, 1993). To index the shrimp spawning stock in the earlier study, I used a simple average of September–October shrimp fishery CPUE. Both indices depended heavily on an assumption of constant

catchability. The recruitment index also relied on an assumption of constant natural mortality.

The relationship between CPUE, population size, geographic stock area, and the catchability coefficient can be described by the equations

$$CPUE = paNA^{-b} \quad (1)$$

$$q = paA^{-b}, \quad (2)$$

where  $p$  = the proportion of shrimp within the sweep of the gear that will be captured (the elemental efficiency);

$A$  = the geographic stock area (stock area);

$a$  = the area covered by a single sweep of the gear;

$b$  = a coefficient that describes how  $q$  will vary with stock area;

$N$  = the population size; and

$q$  = the catchability coefficient (Winters and Wheeler, 1985).

Accordingly, an assumption of constant catchability is equivalent to assuming that stock area is constant. However, stock area for ocean shrimp has been shown to be roughly proportional to stock abundance and to vary substantially between years (Hannah, 1995; Hannah, 1997). In the present study, I incorporated stock area estimates into both the shrimp recruitment and spawner indices, making an assumption of constant catchability unnecessary. I did assume that  $b$  in the above equation was equal to 1, an assumption that has been previously shown to be reasonable, according to a roughly linear relationship between stock area and abundance (Hannah, 1995). My approach also assumes that the elemental efficiency of shrimp trawl gear,  $p$ , is constant.

Because the assumed rate of natural mortality was used in the prior study (Hannah, 1993) only to discount age-1 catches forward in time to 1 April of the age-2 year, the simplest way to reduce the influence of variable natural mortality on the recruitment index is to index the population at an earlier age. This is a useful approach; however, age-1 shrimp must still be fully recruited to the fishery at the time chosen. Using data from the early years of the shrimp fishery, Lo (1978) showed that age-1 shrimp were incompletely recruited to the California shrimp fishery, especially early in the April–October season. A variety of data suggest that, since about 1979, age-1 shrimp have been fully recruited to the trawl fishery by June or July of each year. Prior to 1974, Oregon required a minimum codend mesh of 34.9-mm (1 3/8 in) stretch measure. Since this date, minimum codend mesh size has been unregulated in the Or-

egon fishery, although California still requires a minimum codend mesh of 34.9 mm. Prior to 1978, shrimp growth was slower (Hannah and Jones, 1991) and age-1 shrimp in the study area (Fig. 1) were clearly not fully recruited to trawl gear until very late in the season (ODFW<sup>1</sup>). After 1978, shrimp growth increased, possibly owing to reduced density from heavy fishing, although other factors were also involved, notably accelerated sex change that may have been a response to reduced numbers of older shrimp (Charnov et al., 1978; Hannah and Jones, 1991). Average codend mesh size in the Oregon fleet also decreased sometime during the 1970s, averaging 30.2 mm by 1981, decreasing to 28.7 mm by 1991–92 (Jones et al., 1996). Accordingly, in this study I chose the August–September time period to index the age-1 shrimp population, and restricted my analysis to the years after 1979. With the months of August–September, the population was indexed eight months earlier than in the previous study, but at a time period late enough that age-1 shrimp could reasonably be assumed to be fully recruited to the trawl gear being fished.

To index shrimp recruitment in the present study, I used the average August–September CPUE for age-1 shrimp only as an index of density and multiplied this index by stock area (ha) for the same year class (Hannah, 1997). In this case, CPUE was expressed as shrimp per hectare trawled, using an average estimate of 5.93 ha trawled per single-rig equivalent hour fished (Hannah, 1995). To account for years in which early season catches of age-1 shrimp were high, I added in the catch of age-1 shrimp for the months of April–July of the same year. Thus, recruitment was calculated as

$$R_t = (D_t A_t) + C_t, \quad (3)$$

where  $R$  = recruitment of age-1 shrimp in year  $t$ ;  
 $D$  = the average fishery CPUE of age-1 shrimp in August and September of year  $t$ ;  
 $A$  = the stock area for the age-1 year class in year  $t$ ; and  
 $C$  = the summed fishery catch of age-1 shrimp in the months April to July of year  $t$ .

Use of these additional catches for April–July does rely on an assumption of constant natural mortality, although the importance of this assumption is clearly reduced. Age-1 shrimp CPUE for Pacific States Marine Fisheries Commission (PSMFC) statistical areas 82–88 was obtained from Zirges et al. (1982) and

<sup>1</sup> ODFW (Oregon Department of Fish and Wildlife). 1981 to present. 2040 SE Marine Science Dr., Newport, OR. Unpubl. data.

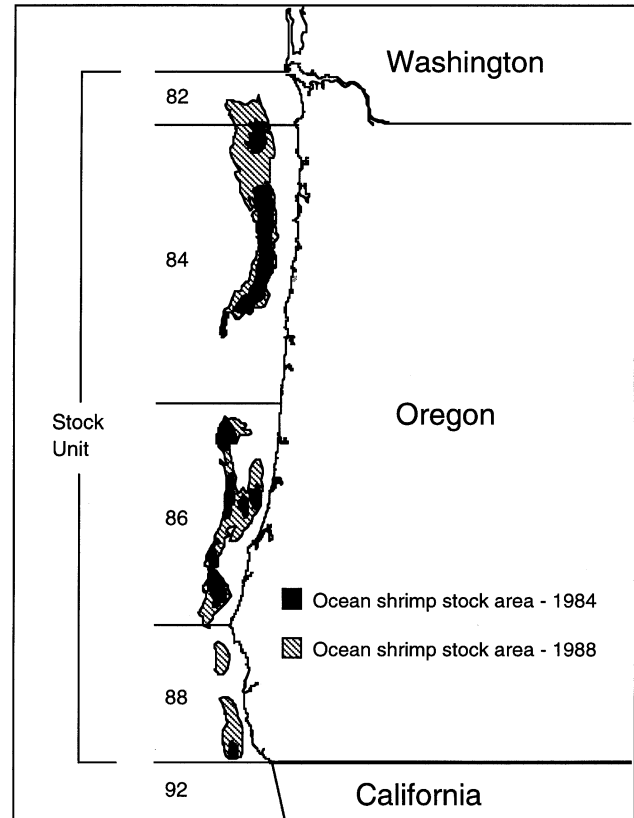


Figure 1

Location of commercial concentrations of ocean shrimp (*Pandalus jordani*) off coastal Oregon, in Pacific States Marine Fisheries Commission statistical areas 82–88. Dark areas show the approximate minimum areal extent of the shrimp grounds (1984) and the lighter shaded areas show the largest areal extent observed from 1980 to 96 (1988).

Hannah et al. (1997). The collection and analysis of biological samples from the commercial catch has been described by Hannah and Jones (1991).

The data used to construct the recruitment and spawning stock indices developed in this study differ in some respects from the data used for the prior recruitment study. In the prior study, logbook data were available from Washington, Oregon, and California, such that a complete accounting of catch and effort was possible for PSMFC areas 82–92 (Fig. 1). Beginning in 1992, logbook data from the states of California and Washington became unavailable. Accordingly, the data used in this study was based on Oregon landings for the entire study period. To minimize the impact of the missing information on the indices developed, the study area was limited to areas 82–88 (Fig. 1). I believe that the missing information will create very minimal error in the new indices for several reasons. First, Oregon landings comprise the great majority of the removals of shrimp from statistical areas 82–88. The average percent-

age of total catch from these areas landed in Oregon from 1980 to 1992 was 92.5% (Hannah et al., 1997). Second, the components of the new indices, with one exception, did not depend on a complete accounting of catch and effort from the study area but simply on a good estimate of average CPUE at age and accurate estimates of stock area. The one component of the recruitment index that was somewhat influenced by the missing catch data was the added age-1 shrimp catch from the months of April–July. A correction for this potential source of error is not available; however, I believe the magnitude of error introduced is likely to be small in relation to the interannual variation in the index itself. The use of CPUE as a direct index of density is equivalent to assuming that elemental efficiency,  $p$  in Equation 2 above, equals 100%. This is clearly not reasonable, however; selecting a value for  $p$  is problematic. The principal importance of selecting a value for  $p$  is to obtain a proper scaling between the two components of the recruitment index: one based on CPUE and stock area; the other based on the early-season catch of age-1 shrimp. Proper scaling of these two components is less critical than it seems at first examination because the two index components are actually closely correlated ( $r=0.774$  at  $p=0.5$ ). Accordingly, a change in the scaling between the two components is expected to have little influence on the pattern of time series variation in the resulting index. As a check on this assumption, all indices using CPUE as a density index in this study were calculated with a range of  $p$ -values, and the results were then examined to see if they were sensitive to assumptions about  $p$ . For the primary analysis, I chose a  $p$ -value of 0.5 and for the sensitivity analysis I used values of 0.25 and 0.75. for  $p$ , following my earlier examination of shrimp mortality rates (Hannah, 1995).

Commercial logbook data were used to generate estimates of stock area for each shrimp year class. The methods used to estimate stock area, including the correction of estimates for variation in sampling rates, are described in detail in Hannah (1997). Stock area was estimated by using logbook data from June of the recruit year through May of the following year, the time period during which age-1 shrimp contribute most heavily and reliably to the catch. For a few of the years in the 1980–96 time series, the fishery failed to target age-1 shrimp adequately, and harvested primarily the remaining age-2 and older shrimp from prior year classes. For those years, stock area was estimated from a linear regression of stock area on a simple virtual population estimate for that year class, as described in Hannah (1997).

To index the ocean shrimp spawning stock, I used an approach similar to that used for the recruitment

index. For each spawning year, I used the average age-specific CPUE in September–October as an index of age-specific density. Once again, these estimates of density were expanded by using assumed levels of elemental trawl efficiency ranging from 0.25 to 0.75, as discussed above. I then multiplied each density index by the stock-area estimate for that year class, as calculated in the year of recruitment. In using this approach I assumed that the geographic distribution of each newly recruited year class was established at settlement and was persistent, and that local shrimp density was modified by fishing and natural mortality. This assumption is supported by several observations, including the obvious autocorrelation in stock area estimates noted previously (Hannah, 1995), the lack of any evidence for migration in this species and the approximately linear relationship between stock area and abundance. There is some evidence from sea bed drifter recoveries (ODFW<sup>1</sup>) that suggests slow gyres in bottom currents may help retain or concentrate shrimp in some of the major shrimp beds. However, it is unknown whether this effect is sufficiently large to actually alter the areal extent of a shrimp year class after settlement.

An egg production index for ocean shrimp was calculated by expanding the spawner index with available shrimp biological data (ODFW<sup>1</sup>). The biological data used included the mean percentage of females and mean female shrimp carapace length, by age, from samples of the fishery in October. For a few years, October samples were unavailable and September samples were used. I used a pooled length-fecundity relationship from Hannah et al. (1995) to estimate mean fecundity for each age group of female shrimp based on mean carapace length data.

The April harvest of egg-bearing females was estimated for the years 1979–95 in a straightforward manner. April shrimp catch, expressed as numbers of shrimp, for each PSMFC statistical area, was obtained from Hannah et al. (1997). Catch in numbers was multiplied by the average percentage of egg-bearing shrimp estimated for each PSMFC area from biological samples of the April catch (ODFW<sup>1</sup>). The catch of egg-bearing shrimp from each of the four areas (Fig. 1) was then summed.

Because the percentage of egg-bearing shrimp declined throughout April, a time-stratified approach was used to estimate the average percentage of egg-bearing shrimp. One problem with this approach is variation in sample coverage. Although the total number of shrimp examined from the April catch has been fairly consistent, averaging about 2900 shrimp from 1980 to 1996, the early and late portions of April have not always been sampled evenly. For example, some years that had excellent sample coverage in

the first two weeks of April had no samples at all for the second half of the month. To make maximum use of the data available, estimates of the percentage of egg-bearing shrimp from individual samples were averaged for the first and second halves of the month, respectively. These semi-monthly figures were then averaged to produce an overall mean percentage of egg-bearing shrimp in the catch for each April. When samples were missing from the latter half of the month, a zero level of ovigerous shrimp was assumed. When samples were missing for the first half of the month, the level of ovigerous shrimp observed for the second half was assumed as a minimum estimate for the first half of April. Accordingly, the estimates presented in the present study are minimum estimates of the catch of egg-bearing shrimp.

To determine when, during the month of April, egg-bearing shrimp had declined to a minimal component of the catch, I constructed a scatter graph of the raw percentages of egg-bearing females by date, using existing data for 1961–97 (ODFW<sup>1</sup>). Area 82 (Fig. 1) was excluded from this analysis because the incidence of egg-bearing shrimp in this area was generally very low in April.

A stepwise process was used to evaluate the relationships between the new recruitment, spawner, and egg production indices, calculated at assumed values of 0.25, 0.50 and 0.75 for trawl efficiency. Following the findings of my earlier study (Hannah, 1993), the first step in this analysis was to regress log (natural log unless noted) recruitment against April SLH at Crescent City, California, to verify that SLH still explained a significant amount of the interannual variation in recruitment. Simple linear regression was used for this test. These SLH data were obtained from the National Oceanic and Atmospheric Administration's Ocean and Lake Levels Division for the years 1979–95, corresponding to age-1 catch years 1980–96. Next, the residuals were examined and compared graphically and by means of linear regression to the spawner and egg production indices, and outliers were examined in light of the estimates of the catch of egg-bearing shrimp in April. Finally, some multivariate models incorporating April SLH and the spawner and egg production indices were fitted by using multiple regression.

Garcia (1983) and others have stressed that many of the stock-recruitment relationships that have been demonstrated for shrimp stocks are really statisti-

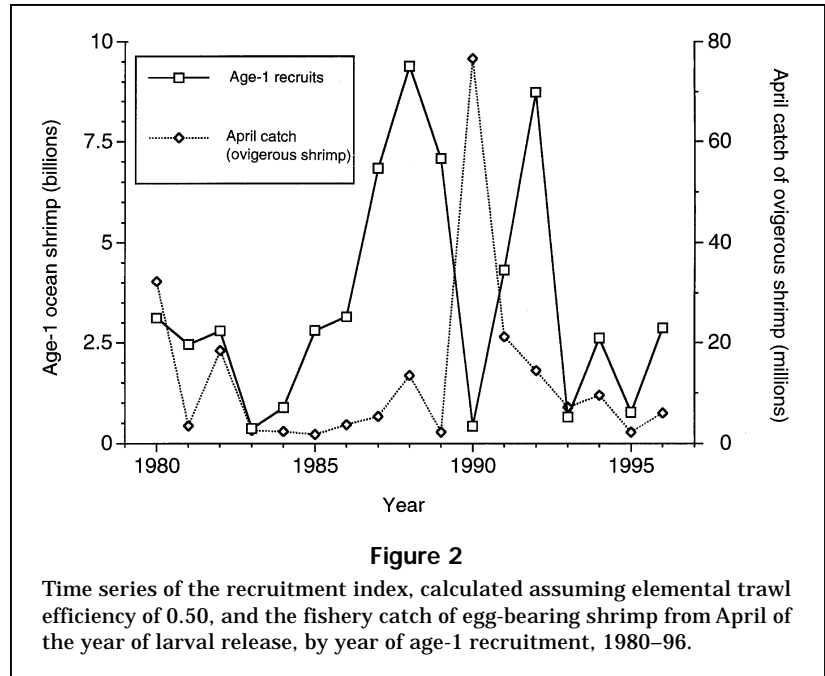


Figure 2

Time series of the recruitment index, calculated assuming elemental trawl efficiency of 0.50, and the fishery catch of egg-bearing shrimp from April of the year of larval release, by year of age-1 recruitment, 1980–96.

cal artifacts caused by a strong recruitment-stock relationship (the reverse of a stock-recruitment relationship, rather spawning stock in year  $t$  as a function of recruitment that same year) in combination with serially autocorrelated, environmentally driven, recruitment. To test for such a possibility in the present analysis of ocean shrimp recruitment, I regressed the new recruitment index against itself at a lag of one year. I also examined the recruitment-stock relationship further by graphically comparing the spawning index, broken out by age class, to the recruitment index from the same year.

## Results

The recruitment index (Fig. 2; Table 1; all indices calculated assuming 0.50 for trawl efficiency, unless noted) shows wide variation in ocean shrimp recruitment, especially after 1986 (year of age-1 recruitment, unless noted). Recruitment in 1983, 1984, 1990, and 1993 was very low, whereas very high recruitment was observed for the 1987–89 and 1992 year classes. These four large year classes had a very significant influence on total landings from the shrimp fishery during the years included in this study. Although they represent less than one third of the years in the time series, they contributed roughly 60% of the total landings of shrimp.

The log of the shrimp recruitment index was strongly negatively correlated with April SLH at Crescent City, California, in the year of larval release

Table 1

Ocean shrimp population data used for regression analyses, including April SLH, geographic stock area (year is June–May), and recruitment, spawner, and egg production indices, by calendar year (no lags). Recruitment, spawner, and egg production indices are calculated assuming elemental trawl efficiency of 0.50.

Year	Recruitment index (millions — age 1)	April SLH (cm)	Geographic stock area (1000 ha)	Spawning abundance (millions)	Egg production (billions)
1979	—	214.9	—	—	—
1980	3122.0	218.2	450.6	—	—
1981	2455.0	210.9	477.2	—	—
1982	2789.1	226.5	344.1	2133.0	2002.9
1983	368.6	229.2	172.9	604.0	717.1
1984	884.5	211.5	158.7	1150.7	1257.4
1985	2798.4	213.1	319.4	3049.7	1913.4
1986	3148.7	212.5	460.5	2293.1	1616.0
1987	6840.2	209.1	464.6	3760.3	2558.0
1988	9388.1	214.9	605.0	7332.6	5783.8
1989	7078.9	222.2	585.1	6872.6	4845.5
1990	429.2	219.2	208.8	1652.2	3583.3
1991	4312.5	212.5	478.1	2141.4	1590.4
1992	8729.9	230.7	406.3	4519.7	4146.1
1993	649.9	227.4	200.8	921.4	1670.2
1994	2608.4	215.0	364.1	1465.3	1291.0
1995	768.6	220.0	215.7	—	—
1996	2862.8	—	362.0	—	—

(Fig. 3). The linear regression model (Table 2; model 1) was highly significant, with April SLH explaining 48% (unadjusted for degrees of freedom, unless noted) of the variation in log recruits. More importantly, the linear relationship is not based heavily on just a few points but appears quite general in nature, confirming a routine relationship between recruitment and April SLH shortly after the peak of larval release.

The residuals from the regression of log recruits on April SLH, graphed against the spawner index, show a pattern that is suggestive of a quasilinear stock-recruitment relationship, with the 1990 year class as an exceptional outlier (Fig. 4). The same residuals regressed against the egg production index show a similar pattern (Fig. 5). The time series of recruitment and the April catch of egg-bearing shrimp from the year of larval release (Fig. 2) shows that the year class released in 1989 (1990 year class) may have been heavily impacted by the trawl fishery, owing to an extremely high harvest of late egg-bearing shrimp. This occurred in combination with a high April sea level, suggestive of a late spring transition (Table 1). Data on the percentage of ovigerous females in the April catch (Fig. 6) suggest that postponement of the opening of the season to April 20<sup>th</sup> each year could eliminate this impact.

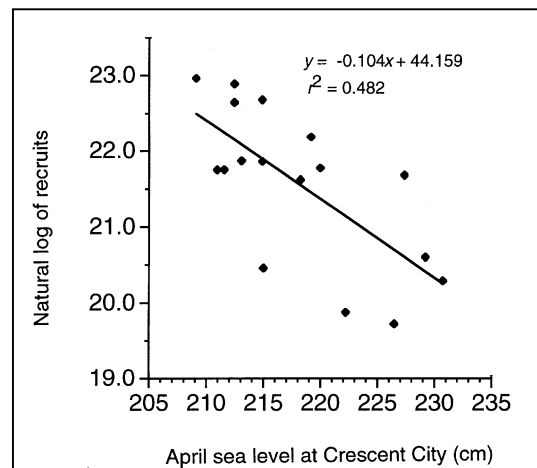
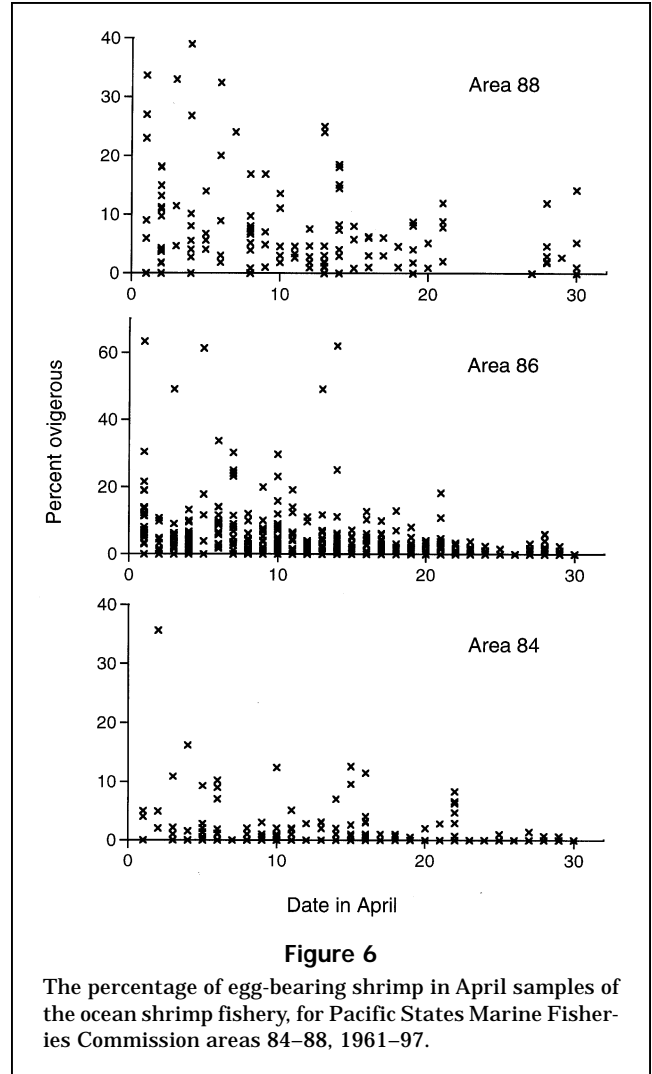
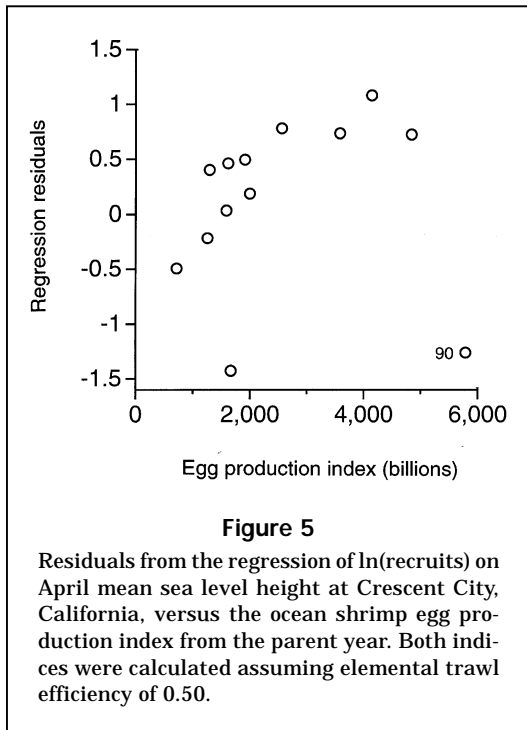
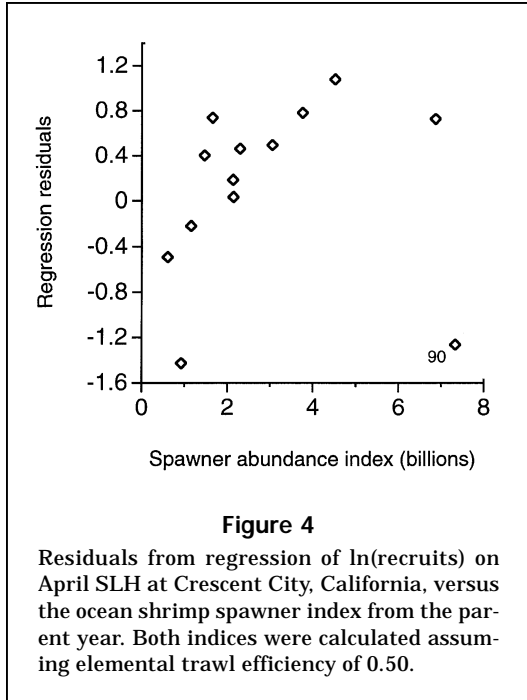


Figure 3

Linear regression of the natural log of the shrimp recruitment index, calculated assuming elemental trawl efficiency of 0.50, versus mean sea level height at Crescent City, California, during April of the year of larval release.

When the 1990 year class was excluded, neither scatter graph (Figs. 4–5) exhibited sufficient evidence of curvature to indicate the most appropriate form



of the stock-recruitment relationship for ocean shrimp. If the 1990 year class was included, the graphs could be interpreted as supporting a dome-shaped stock-recruitment curve, or could even be interpreted as evidence of no relationship between stock and recruitment at all. Given the extremely large fishery impact on egg-bearing females in the

spring of 1989 (Fig 2), in combination with the fact that April has been shown to be a critical period for larval survival, excluding the 1990 data point seems the most conservative approach. With the 1990 year class excluded, a multivariate model incorporating April SLH and the log of the spawner index, was highly significant ( $P < 0.001$ ) and explained 79% of the variation in log recruitment (Table 2, model 2). The comparable multivariate model, incorporating the egg production index, was also highly significant ( $P < 0.01$ ) and explained 68% of the variation in log recruitment (Table 2, model 3). Both models incorporated April SLH and log spawners or eggs with negative and positive slopes, respectively. A linear regression of the recruitment index on itself, at a lag of one year, was nonsignificant ( $P > 0.05$ ) and showed little evidence of serial autocorrelation, suggesting that the evidence presented in Figures 4 and 5, for a statistical dependence of recruitment on parent stock in ocean shrimp, may be valid.

Table 2

Results of univariate and multivariate regression analysis. Dependent variable is the natural log of the ocean shrimp recruitment index in year  $t$ . All population indices are calculated assuming elemental trawl efficiency of 0.50.

Parameters and variables	Coefficients	95% CI	F-value	R <sup>2</sup> (adjusted)	P>F
<b>Model 1</b>					
Intercept	44.159				
April SLH <sub><math>t-1</math></sub>	-0.104	±0.059			
Full Model			13.983	0.448	0.0020
<b>Model 2 (1990 excluded)</b>					
Intercept	29.108				
April SLH <sub><math>t-1</math></sub>	-0.112	±0.047	29.388		0.0004
Ln (spawner index) <sub><math>t-2</math></sub>	0.796	±0.502	12.893		0.0058
Full Model			16.550	0.739	0.0010
<b>Model 3 (1990 excluded)</b>					
Intercept	21.636				
April SLH <sub><math>t-1</math></sub>	-0.103	±0.056	17.528		0.0024
Ln(egg index) <sub><math>t-2</math></sub>	0.799	±0.754	5.743		0.0401
Full Model			9.676	0.612	0.0057
<b>Model 4</b>					
Intercept	27.531				
April SLH <sub><math>t-1</math></sub>	-0.119	±0.053	26.037		0.0006
Ln(spawner index) <sub><math>t-2</math></sub>	0.957	±0.628	11.879		0.0073
April catch of ovigerous Shrimp <sub><math>t-1</math></sub> (millions)	-0.035	±0.022	13.006		0.0057
Full model			11.956	0.733	0.0017

A multivariate model, using the complete data series and incorporating April SLH, the natural logarithm of the spawner index, and the April catch of egg-bearing shrimp from the year of larval release, was also highly significant ( $P < 0.005$ ) and explained 80% of the variation in log recruitment (Table 2, model 4). As expected, the coefficients for SLH and the catch of egg-bearing shrimp in April of the release year were both negative, whereas the coefficient for the natural logarithm of spawners was positive. Fitting this three-variable model, with the 1990 year class excluded, resulted in the catch of egg-bearing shrimp not contributing significantly to the overall model fit, suggesting that this variable does not have general predictive value for the recruitment time series but is useful only in explaining the very low recruitment in 1990.

Despite efforts to de-emphasize the importance of age-1 catches in the recruitment series by indexing the stock at an earlier age, these early catches still represented a large component of the index (Fig. 7). This finding suggests that the assumption of constant natural mortality could still be inducing errors

in the recruitment index. However, when the analyses discussed above were conducted on the recruitment index excluding the April–July age-1 catches, the results were very similar. This similarity argues that the findings of this study are not sensitive to failure of the assumption of constant natural mortality, as it is employed in calculating the recruitment index. The results were also insensitive to the assumed level of elemental trawl efficiency (Table 3, models 5 and 6).

The data in Figure 4 suggest that if shrimp spawner abundance could be maintained above some threshold (about 1.3 billion shrimp for an assumption of 0.50 for elemental trawl efficiency), the ability to produce large shrimp year classes in favorable environmental conditions could be preserved in all years. A similar threshold could also be identified in terms of egg production (Fig. 5). Examination of the relationship between age-1 spawners, older spawners, and the recruitment index from the same calendar year (Fig. 8), suggests a strong recruitment-stock relationship for ocean shrimp and a minor role for the fishery in determining spawner abundance. In



Table 3

Results of multivariate regression analysis using alternative assumed values for elemental trawl efficiency. Dependent variable for models 5 and 6 is the natural log of the ocean shrimp recruitment index in year  $t$ , calculated assuming elemental trawl efficiency of 0.25 and 0.75, respectively.

Parameters and variables	Coefficients	95% CI	F-value	$R^2$ (adjusted)	$P>F$
Model 5 efficiency of 0.25					
Intercept	27.583				
April $SLH_{t-1}$	-0.122	$\pm 0.056$	24.306		0.0008
Ln (spawner index) $_{t-2}$	0.976	$\pm 0.666$	11.022		0.0089
April catch of ovigerous Shrimp $_{t-1}$ (millions)	-0.038	$\pm 0.024$	13.252		0.0054
Full model			11.500	0.724	0.0020
Model 6 efficiency of 0.75					
Intercept	27.437				
April $SLH_{t-1}$	-0.117	$\pm 0.051$	26.829		0.0006
Ln (spawner index) $_{t-2}$	0.946	$\pm 0.608$	12.378		0.0065
April catch of ovigerous Shrimp $_{t-1}$ (millions)	-0.034	$\pm 0.022$	12.683		0.0061
Full model			12.107	0.735	0.0016

each of the years in which spawner abundance falls below the proposed threshold, there was a serious recruitment failure, depressing the age-1 population. In the case of spawn-year 1984, two year-class failures in a row were evident. All of the very low year classes shown in Figure 8 coincide with high April SLH the prior year (Table 1), suggesting that most low spawner abundances were largely the result of environmental forcing and a strong recruitment-stock relationship. Two of the years shown, 1984 and 1993, followed the major El Niño southern oscillation (ENSO) events of 1982–83 and 1992–93, and likely resulted from the rise in sea levels and accelerated northward currents often associated with these events and their likely influence on conditions in April (Huyer et al., 1979; Chelton and Davis, 1982; Chelton et al., 1982; Huyer and Smith, 1985).

However, the data suggest that the fishery does play some role in creating the low spawner abundances shown in Figure 8. Although the low recruitment in 1990 corresponds to a poor spring transition in 1989 (Table 1), the data suggest that the high harvest of egg-bearing females in April of 1989 exacerbated this recruitment failure (Fig. 2; Tables 1 and 2), subse-

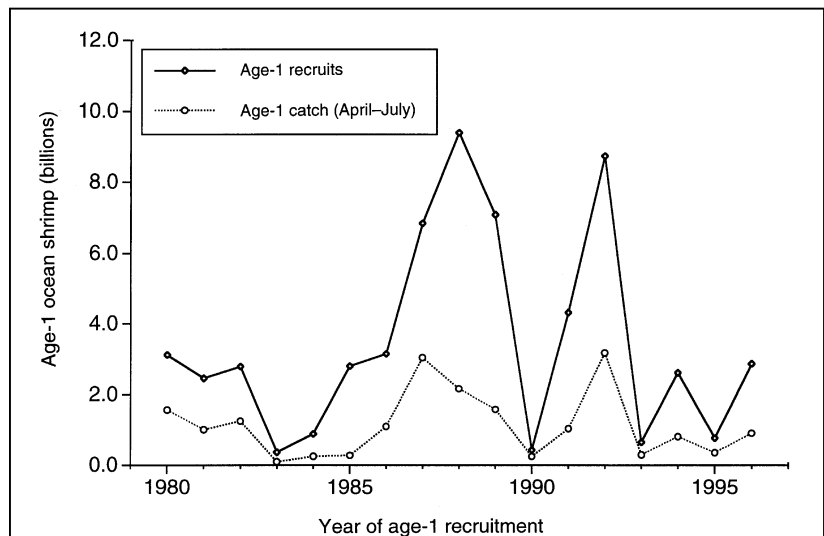


Figure 7

Age-1 ocean shrimp recruitment index, calculated assuming elemental trawl efficiency of 0.50, and the portion of the index for the April–July catch of age-1 shrimp, by year, 1980–96.

quently depressing spawner abundance (Fig. 8). The large difference between age-1 recruitment and the age-1 component of the spawner index in 1993 (Fig. 8) also suggests that spawner abundance may have been depressed by the fishery in that year. The close association between a year-class failure and low spawning abundance the same year also demon-

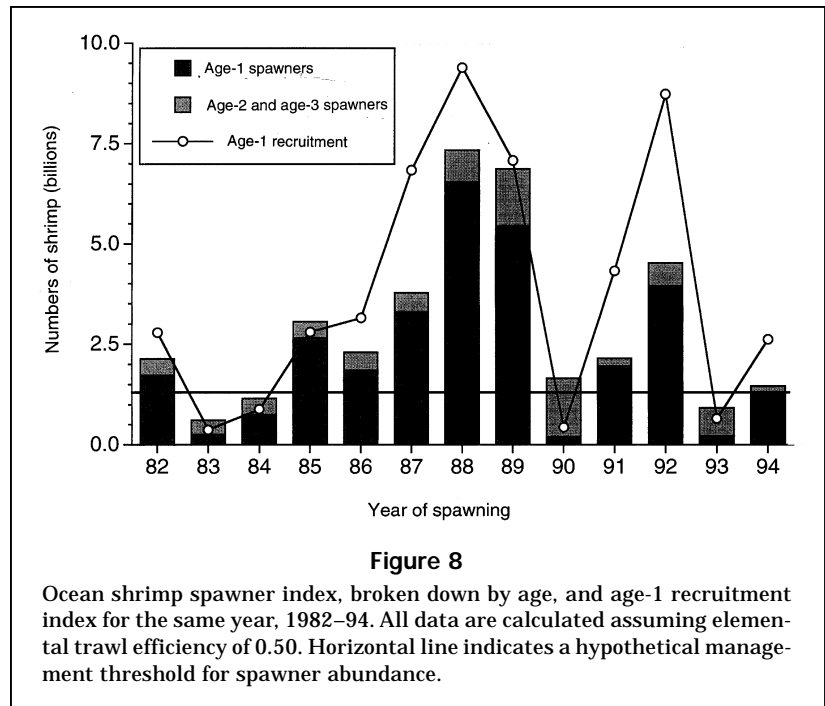
strates that attempting to maintain a spawner threshold by increasing escapement of age-1 shrimp is unlikely to be an effective management strategy. The reason for this is that precisely when a boost in spawner abundance is needed, the age-1 year class is too depressed to offer significant help, even with a complete cessation of fishing. This result suggests that when a year-class failure is detected in this stock, reducing fishery impacts on all age classes of shrimp may be a better strategy to maintain spawner abundance than the standard management measures (e.g. minimum codend mesh or maximum count per pound) which protect the escapement of age-1 shrimp.

## Discussion

This analysis supports the hypothesis that the spring transition in coastal currents is important for successful ocean shrimp recruitment (Hannah, 1993). Although data from this effort and the prior study overlap for 10 of the 16 years presented here, new methods were used in this study that did not depend on constant catchability and were insensitive to failure in the assumption of constant natural mortality and insensitive to assumptions about trawl efficiency. The fact that this study and the earlier effort both found a strong correlation between recruitment and SLH in April of the year of larval release suggests that the interannual variation in shrimp recruitment is substantial, creating a strong "signal" that can be observed through considerable "noise" from various simplifying assumptions.

The precise mechanisms by which a large drop in spring sea levels coincides with strong recruitment of ocean shrimp remains a matter for speculation. This study did not attempt to investigate this issue. A more in-depth discussion of the alternative hypotheses can be found in the earlier paper (Hannah, 1993). The continued importance of April SLH as a strong correlate of shrimp recruitment suggests that further investigation of the potential mechanisms is warranted.

The principal novel finding of this study is the evidence for a stock-recruitment relationship for ocean shrimp. This evidence is statistical in nature and the data series is fairly short, suggesting that this finding should be considered preliminary at this time. The fact that much of the environmental variation



in recruitment has been accounted for in the models, in combination with the lack of a serial autocorrelation in the recruitment index, supports the contention that an actual stock-recruitment relationship has been detected (Garcia, 1983). The form of the detected relationship corresponds to the ascending leg of the curve, indicating that some reduction in average recruitment has resulted from low spawner abundance. Unfortunately, the relationship demonstrated gives little indication of the shape of the right hand portion of the curve, leaving the proper functional form an open question.

With environmental variation strongly influencing ocean shrimp recruitment, the detection of a stock-recruitment relationship has different implications from those in a classical application of stock-recruitment theory. In stocks with reasonably stable recruitment, stock-recruitment curve parameters can, in theory, be used to determine a maximum sustainable yield. For shrimp, the multivariate recruitment models (Table 2) define a surface over which recruitment varies in response to the environment and changes in the level of spawning stock. The environmental influence on recruitment also implies a very strong recruitment-stock relationship; the points residing in the lower left corner of Figure 4 are not simply the result of fishing but are due to low recruitment in the parent years, in combination with fishing (Fig. 8). The main value of knowing that a stock-recruitment relationship exists for ocean shrimp is that it suggests strongly that there is a

level of fishing beyond which the average subsequent recruitment will be reduced. The distribution of stock and recruitment data in this study suggests that maintaining a "spawner threshold" for this stock unit should produce higher average recruitment (Fig. 4). The threshold suggested here, 1.3 billion spawning shrimp is, of course, not an absolute measure, but rather a level that is relevant only to the indices as constructed here, assuming elemental trawl efficiency of 0.50. If better information on the average elemental efficiency of shrimp trawl gear can be developed, then an actual spawning threshold can be calculated. With or without an absolute threshold, these data suggest that curtailing harvest in years of recruitment failure has the potential to increase subsequent average recruitment.

One seemingly surprising finding of this study is that egg production seems to offer little benefit over spawner abundance as an index of shrimp reproductive output. This result is partially an artifact caused by the two indices being based on the same underlying estimates of stock area and density, in combination with the use of a static length-fecundity relationship based on pooled data from several samples (Hannah et al., 1995). The egg production index incorporates only two additional sources of real variation: the variation found in the average size of females and in the percentage of females in the spawning population, and these parameters are not highly variable (Hannah et al., 1995). The finding that egg production estimates offer little benefit over estimates of spawner abundance is also convenient because the flexible sex change exhibited by ocean shrimp makes it difficult to translate an egg production goal into a quantity that can be used to directly manage the fishery, such as a biomass threshold (Charnov et al., 1978; Hannah and Jones, 1991). To do so would require a way to accurately forecast the percentage of both primary females and age-2 males in the fall of the year, a technique not presently available.

The apparent influence of intense fishing on late egg-bearing females in April may have important implications for management of the ocean shrimp stock and suggests an important interaction between recruitment, parent reproductive output, and variation in the ocean environment. If the timing of the spring transition is indeed the critical determinant of ocean shrimp larval survival, then larvae released early and late in the spring may suffer very different fates, depending on when the spring transition occurs. When the transition is late, logic suggests that the magnitude of recruitment may depend very heavily on the survival of late release larvae, the very ones the fishery is capable of impacting heavily by harvesting egg-bearing shrimp. If this hypothesis is

correct, it also suggests that environmental variation and the various measures of shrimp reproductive output one might use are confounded. For example, a large larval release in a year with a late transition may be the functional equivalent of a much smaller larval release in a year with an early transition; both result in low numbers of larvae released into favorable ocean conditions. Similarly, the impact on recruitment of harvesting late egg-bearing females could be large or minimal depending on the timing of the transition. For the 1989 year class, the impact was apparently quite severe, owing to a combination of a large catch of egg-bearing shrimp and a moderately high April sea level (Table 1), suggesting a late spring transition. The same amount of harvest may have had minimal impact on recruitment in a year with an early spring transition, when this hypothesis suggests that most of the larvae would have already been released into favorable conditions. Upon close examination, the interaction between variation in the timing of the spring transition and the timing and magnitude of larval release makes it unlikely that any simple measure of reproductive output would have direct explanatory power with regard to the level of subsequent recruitment. Such a mechanism could also be operating to obscure the stock-recruitment relationship in other stocks with an early critical stage and environmentally forced recruitment.

I consider the detection of a stock-recruitment relationship for this species to be a preliminary finding at this time. If this result endures as additional data become available, the implications for management of the ocean shrimp stock are still not entirely clear. Regulations aimed at eliminating, or severely reducing, the harvest of egg-bearing female shrimp in April may help increase average recruitment of ocean shrimp, with very little reduction in short-term yield. If the opening date of the ocean shrimp season were delayed 2–3 weeks, the harvest of egg-bearing shrimp in April would be virtually eliminated in areas 84 and 86 (Fig. 6). In more southern areas, like area 88, a full month delay is needed to eliminate harvest of egg-bearing shrimp (Fig. 6). With 6 months of fishing remaining in the open season, it is unlikely that annual exploitation rates would be greatly affected by a delay in the season opening date. Although major benefits from such a change in management would not accrue in most years, the evidence for a general stock-recruitment relationship suggests that some small increase in long-term average recruitment would result.

The other novel finding of this study concerns the strong recruitment-stock relationship for ocean shrimp, and its implications for managing highly variable, short-lived stocks. The data show that most

(2 of 3 observed) years of low spawner abundance result mainly from recruitment failures at age 1. This finding suggests that the classic management strategies, aimed at maintaining age-1 escapement rates, such as maximum count-per-pound and minimum codend mesh size, are unlikely to be very successful at reducing recruitment variability and increasing average recruitment for ocean shrimp. The reason for this is that by allowing increased escapement from an extremely depressed year class, there will be likely little impact on total spawner abundance. Rather, a strategy that reduces or eliminates exploitation of all age classes, once a year-class failure has been detected, has more potential to increase spawner abundance, simply because the remaining older shrimp may be more abundant than the failed age-1 year class. Another alternative, of course, is to manage at much lower exploitation rates, such that more shrimp survive to spawn at ages 2 and 3, although such a strategy is unlikely to maximize yield. The precise impact on yield of such an approach is difficult to predict without better knowledge of natural mortality rates. Natural mortality rates of ocean shrimp have been shown to vary widely, possibly in response to changes in the abundance of predator stocks (Hannah, 1995), such as Pacific whiting (*Merluccius productus*). Improved estimates of natural mortality rates for shrimp in turn depend on better knowledge of the elemental efficiency of shrimp trawl gear (Hannah, 1995). In addition, changes in management of this fishery should be geared towards maximizing economic rather than biomass yield (PFMC, 1981), suggesting that a comprehensive bio-economic model is needed before the findings of this study can begin to be used.

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