Abstract.–The trawl fishery for ocean pink shrimp (*Pandalus jordani* Rathbun) has increased dramatically since the early 1970s. Catch and effort statistics and catch sampling data from 1968-88 were analyzed to evaluate changes in the shrimp population structure. Carapace length at age one and two have increased significantly since 1978, concurrent with a reduction in fishery catch per unit effort, strongly indicating density-dependent growth. The seasonal pattern of growth provides further evidence for density-dependent growth. The number of age three shrimp in the catch has declined markedly since 1978, while age one shrimp have increased from 30.6% of the catch to 69.2%. The percentage of age one shrimp maturing as females has increased to 30-50% in some years, while the overall percentage of males shows no trend. The changes in growth, and age and sex composition of the catch are attributed in part to the impact of the trawl fishery, which is currently continuing to intensify. Density-dependent growth, and the ability to accelerate the sex change process make pink shrimp resistant to over-harvest. However, at some exploitation level the reduction of the age 1 spawning stock should begin to reduce subsequent recruitment. Recent strong year classes indicate that the fishery probably has not reached that level of exploitation.

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Fishery-induced Changes in the Population Structure of Pink Shrimp *Pandalus jordani*

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The Pacific trawl fishery for pink shrimp *Pandalus jordani* Rathbun has developed from a fishery with landings of around 220 mt in the early 1960s to a fishery regularly landing in excess of 18,000 mt. In six of the thirteen years since 1975, combined landings for the states of California, Washington, and Oregon have exceeded 24,000 mt. Pink shrimp range from San Diego, California to Unalaska, Alaska (Butler 1964); however, the majority of the catch is taken between Cape Mendocino, California and Destruction Island, Washington. The development of the fishery has been well summarized by Dahlstrom (1970), Fox (1972), Zirges and Robinson (1980), and others.

Saelens and Zirges (1985) described the 1984 fishery for pink shrimp and suggested that there was some evidence of changes in the shrimp population structure that were possibly the result of fishing. They noted improved growth and higher levels of age-1 shrimp in the catch, relative to earlier years. Fishing effort and shrimp catch have continued to increase since 1984. Given the continued development of this fishery, we felt that some fishery-induced changes in the population structure would be evident in a thorough review of the fishery sampling data. We examined 23 years of information from the pink shrimp fishery off the coasts of Oregon and northern California to search for the classic population responses to increased fishing. Specifically, we looked for persistent shifts in age and sex composition, changes in the age of female maturity, evidence of reduced stock biomass, and improved shrimp growth as a response to lower biomass. As a final step, we attempted to relate the observed changes to the development of the fishery and alternatively to environmental factors.

Methods

We examined monthly sample data from the landed catch of pink shrimp for the years 1966–88. The data is comprised of several samples from each statistical area (Fig. 1) and month of the fishing season. The season currently runs from April through October, but has been longer in the past. Individual samples for each area and month (area–month) were combined for analysis of age and sex composition. Sample summaries provide individual carapace lengths and average weight expressed as the number of whole shrimp per pound. Shrimp are classified as male, female, or transitional based upon close examination of the inner ramus of the first pleopod (Tegelberg and Smith 1957). Shrimp age is determined by modes in the combined length-frequency histogram (Zirges et al. 1981). Nadirs in the histograms define the range of carapace lengths corresponding to each age group, then ages are assigned to individual shrimp.

Zirges et al. (1982) concluded that pink shrimp from statistical areas

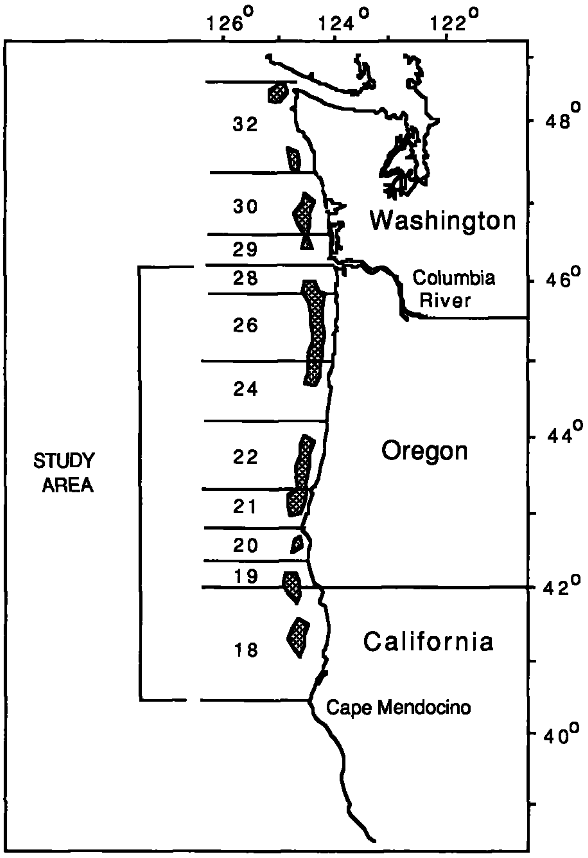

Figure 1
Location of commercial concentrations of pink shrimp *Pandalus jordani* along the U.S. Pacific coast (shaded areas) and statistical areas 18–32.

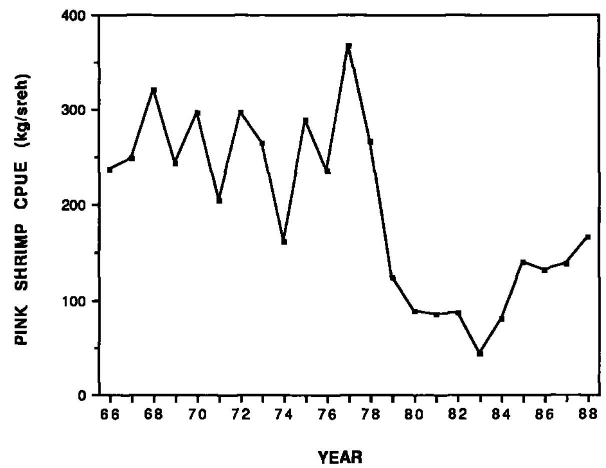

Figure 2
Catch-per-unit-effort (kg/single-rig equivalent hour) for the pink shrimp fishery in statistical areas 18–28 for the years 1966–88.

18–28 constituted a single stock, based upon an analysis of growth, maturation rates, and coastal oceanographic conditions. We used the same stock unit to allow us to draw upon the summarized sample data from Zirges et al. (1982) for the years 1966–81.

To evaluate the effect of shrimp density on growth, we compared shrimp carapace length at age for two time-periods representing different levels of population biomass. We use the term "density" in the sense of biomass per unit area rather than the number of individuals per unit area. We used catch-per-unit-effort (CPUE) as our index of shrimp density.

During the years 1975–78 major improvements in trawl design were implemented by the shrimp industry. Prior to 1976, the predominant shrimp net was a 57-foot (headrope) Gulf of Mexico style, Marinovitch trawl, with a 4-foot vertical opening (Zirges and Robinson 1980). During the years 1975–78 the majority of the fleet switched to locally produced 70–90 foot (headrope) box trawls. The new trawls have proven to be much more efficient for pink shrimp. Besides being generally bigger, they open to a height of 12–18 feet, improving fishing for pink shrimp, which come up off the bottom under reduced light conditions. Increased cloud cover and time of day were shown to bring concentrations of shrimp up off the bottom at least 8 feet (Beardsley 1973). The Oregon box trawls are also constructed differently from the Marinovitch trawls. They are much longer, employ a slower taper, and are hung with considerable "slack" webbing, all contributing to a much more efficient trawl for pink shrimp. The effort data series is not corrected for these gear improvements. Therefore, CPUE data understate the magnitude of biomass reduction since 1978 (Fig. 2). Accordingly, we tested growth for the two time-periods, 1966–78 and 1979–88. We considered these periods to be representative of the virgin stock biomass and the reduced biomass, respectively. We used F-tests to identify significant differences in length at age.

Four area-months were selected as indices for analysis of age-1 and -2 shrimp growth, based upon the completeness of the time-series data. For age-1 shrimp, the months of April–June were excluded because in some years age-1 shrimp are not fully recruited to the trawl gear in those months. For age-2 shrimp, the months of September and October were excluded because in recent years age-2 and older shrimp comprise a small percentage of late-season catches. Given these criteria, the index area-months selected for age-1 shrimp were

Area 22–August, Area 21–July, Area 26–August, and Area 19–August. The most complete time-series for age-2 shrimp were found to be Area 19–August, Area 22–April, Area 21–June, and Area 26–May. Age-2 length comparisons are not independent of the age-1 results. The age-2 analysis was employed to help rule out any apparent changes in growth of age-1 shrimp caused by changes in fishery or gear selectivity over time.

To further investigate factors influencing age-1 shrimp growth, we conducted some exploratory correlation analysis. Since the time-series for the most complete index areas still contained some missing samples, and since many of the environmental factors we wished to test are not area-specific, it was desirable to combine our four age-1 growth indices into one, more complete, time-series. Carapace length at age in pink shrimp exhibits a gradient effect increasing from north to south along the coast and also increasing through the season. To remove these effects and yet preserve the interannual variations in size, one of the four indices was chosen as a standard and the other three were adjusted by an additive factor equal to the difference between the mean of the chosen standard and that of the individual index area–month. Subsequently, the adjusted index area–months were averaged into one time-series. Area 22 was chosen as the standard, and the resultant time-series for age-1 was without gaps and most points were based on two or more adjusted means.

Linear regression was used to examine factors influencing variation in this age-1 shrimp growth index. The independent variables tested included sea surface temperature at Charleston, Oregon (Oreg. Dep. Fish. Wildl., unpubl. data) upwelling at 45°N, 125°W (Bakun 1973; NMFS Pacific Environ. Group, Monterey, CA, unpubl. data), inverse-barometer corrected sea level at Newport, Oregon, (Pittock et al. 1982; Pittock, unpubl. data), and catch per unit effort in the fishery as an index of shrimp density. Kruse (1981) found inverse barometer-corrected sea level at Newport and Neah Bay to be highly correlated with sea-bottom shelf temperatures near Newport. We tested each variable with no time lag (year t) and a 1-year time lag (t – 1) to match growth in an earlier life stage. Adjusted sea level at Newport was tested both with and without the 1983 data point, a year of abnormally high sea level caused by a strong El Niño event. Finally, we tested the average CPUE for the years t and t – 1 combined, to represent the average density encountered over the life of an age-1 shrimp. Second-order polynomial regression was also used to test each variable for a significantly curvilinear relationship with the age-1 growth index (Ricker 1975).

Correlation analysis with time-series data of short duration is often of limited value, but does help to generate initial hypotheses to be tested with the accumulation of future data (Ricker 1975). Short time-series often exhibit unidirectional time trends causing spurious correlations. For these reasons, we felt that correlation analysis would be a relatively poor tool for differentiating the relative importance of the various factors to shrimp growth, but would help to identify the factors which deserve future analysis. Consequently, correlation analysis was not pursued further in this study.

For analysis of trends in the sex composition data, we once again relied upon four index–area months with the most complete time-series. The four index–areas employed were Areas 19 and 28 in October and Areas 21 and 22 in September. Pink shrimp are protandrous hermaphrodites and mate primarily in September and October each year (Pacific Fisheries Management Council 1981). They usually mature first as males in the fall at about 1½ years of age, and after spawning

Table 1

Comparison of mean carapace length for age-1 and -2 pink shrimp for the years 1966–78 and 1979–88 (single classification ANOVA with unequal sample sizes).

Area–Month	Years	Mean carapace length (mm)	*N* (years)	*F* value	*P*>*F*
Age 1					
Area 22–August	1966–78	16.04	13	23.40	0.0001
	1979–88	17.32	7		
Area 21–July	1966–78	15.65	9	6.11	0.0251
	1979–88	16.44	9		
Area 26–August	1966–78	15.56	9	14.09	0.0021
	1979–88	16.67	7		
Area 19–August	1966–78	16.44	8	27.07	0.0002
	1979–88	17.79	7		
Age 2					
Area 19–August	1966–78	19.98	8	76.43	0.0001
	1979–88	21.84	7		
Area 22–April	1966–78	18.03	13	26.70	0.0001
	1979–88	19.59	9		
Area 21–June	1966–78	19.01	8	37.57	0.0001
	1979–88	20.60	9		
Area 26–May	1966–78	18.75	11	7.98	0.0112
	1979–88	19.69	9		

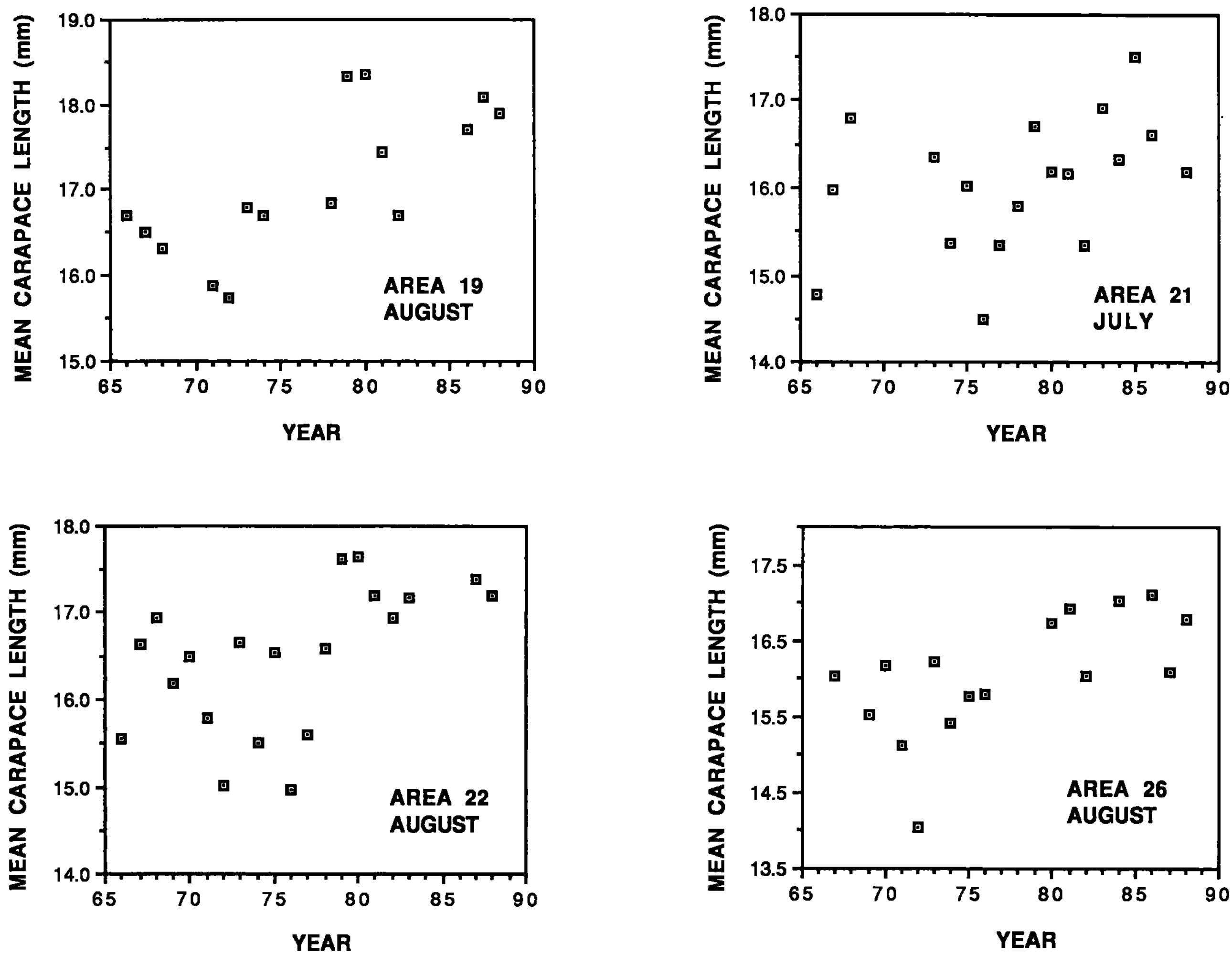

Figure 3
Mean carapace length of age-1 pink shrimp from 1966–88 for the selected index area-months.

go through a transitional phase, usually maturing as a female the following year at age 2½. Age-1 shrimp that mature directly into females, bypassing the male phase, are called primary females. We examined the data for trends in the percentage of primary females and the overall percentage of male shrimp.

Results

We found significantly improved growth of pink shrimp for the 1979–88 period as compared with the 1966–78 period. Mean carapace lengths for all four age-1 index area-months were significantly greater in 1979–88 (Table 1, Fig. 3) based on two-tailed F-tests. Mean carapace lengths were also greater for the four age-2 index area-months (Table 1, Fig. 4). Since age-2 shrimp are fully recruited to the trawl gear, this result rules out any apparent increase in mean length due to fishery or gear selectivity or accelerated sex change of age-1 shrimp. The time-series of catch per unit effort (Fig. 2) indicates that the population biomass has been reduced since 1978.

The increase in growth demonstrated for the 1979–88 catch years represents a substantial increase in average weight. Using the age-1 composite growth index, the mean carapace length of age-1 shrimp has increased from 16.1 to 17.4mm. From the length-weight relationship developed by Zirges et al. (1982);

$$\ln W = -7.94746 + 3.2097 \ln L,$$

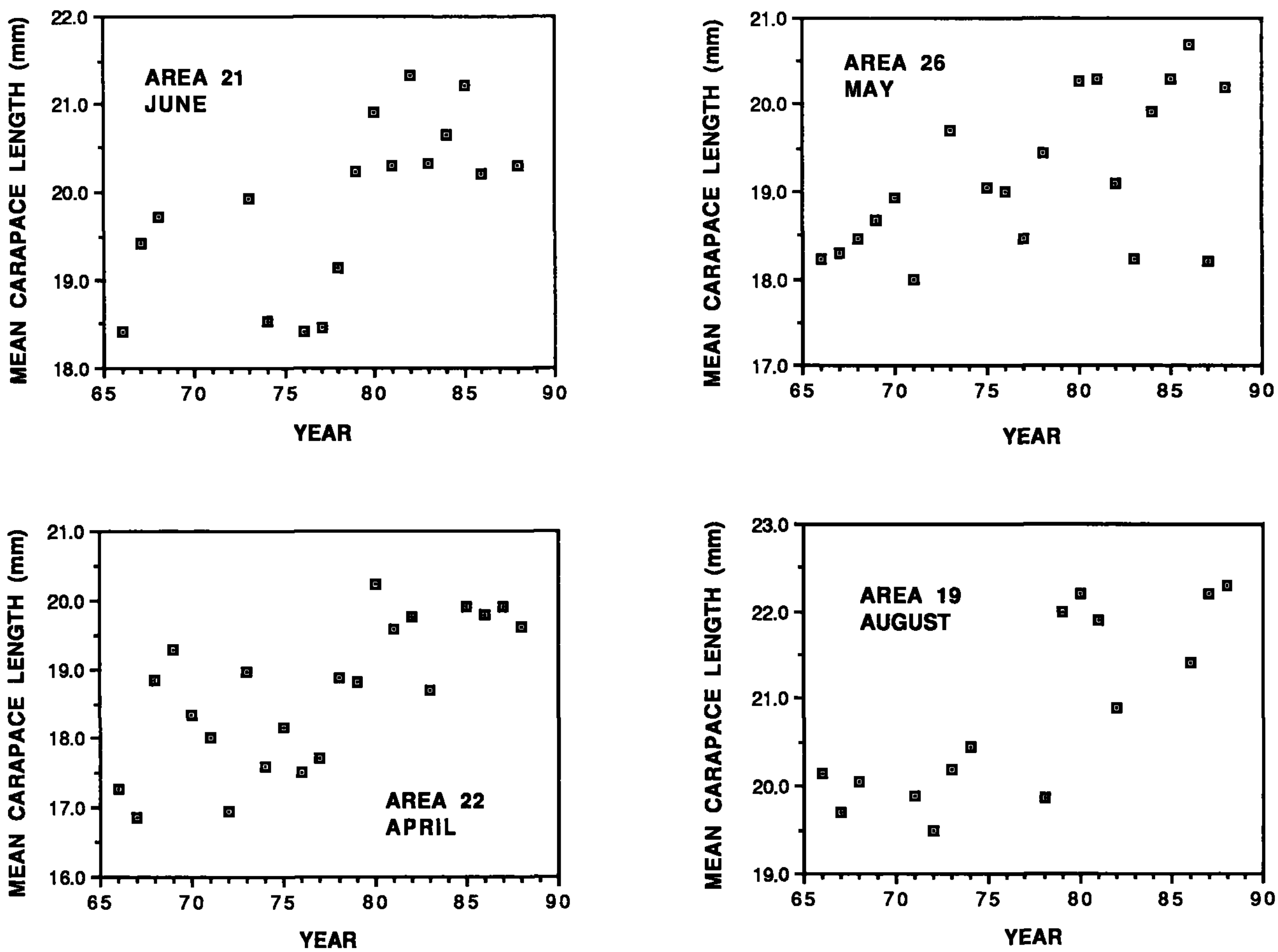

Figure 4
Mean carapace length of age-2 pink shrimp from 1966–88 for the four index area-months.

where W = Weight (g), and
L = Length (mm),

this represents a 28.4% increase in mean weight at age. This is an approximate figure scaled for Area 22 data; however, other areas yield similar results.

The exploratory correlation analysis (Table 2) shows that sea surface temperature at Charleston, Oregon, and sea level at Newport, Oregon (Fig. 5), are positively correlated with the age-1 growth index. However, CPUE (Fig. 6) is negatively correlated with the age-1 growth index suggesting density-dependent growth.

Adjusted sea level at Newport and sea surface temperature at Charleston displayed evidence of a curvilinear relationship, of decreasing slope, with the age-1 growth index. However, the regression coefficients of the second-order polynomial regressions were only significantly different from zero (t-test, P>0.05) for adjusted sea level in year t – 1. The curvature of this relationship is strongly influenced by a single outlier, the 1983 sea level, data point. With this point deleted, the coefficients of the polynomial regression are not significantly different from zero, while the adjusted r-squared value for the simple linear regression increases to 0.528 (Table 2). This suggests that bottom temperature is also influencing shrimp growth.

Graphs of mean length at age for areas 19, 21, 22 and 26 (Fig. 7) show that much of the difference in growth between the 1965–76 and 1977–86 broods is already apparent at age-13 months when the fishery first catches age-1 shrimp. This is not surprising, since density-dependent growth has been demonstrated more frequently for species during the immature phase, with density-dependent changes in fecundity more prevalent in the adult phase (Bailey and Almatar 1989). With the exception of area 19, the curves for the

1965–76 broods show some tendency for the rate of increase in length to slow in the fall, near the end of the fishing season, at ages 17–19 and 27–30 months. The curves for the 1977–86 broods differ somewhat in that this slowing of growth in the fall is less pronounced. These data suggest that density-dependent growth in pink shrimp may continue into the adult stage.

The impact that the trawl fishery has had upon the shrimp population is very evident from an examination of age composition of the catch (Fig. 8). In catch years 1966–78, age-3 shrimp comprised an average 20.4% of the catch by number, falling to an average 4.9% for the years 1979–88. Conversely, age-1 shrimp have risen from an average 30.6% in the early period to 69.2% of the catch in recent years. The increases in relative abundance of age-1 shrimp may be explained in part by the fact that they are recruited to the trawl gear earlier in the season due to increased size at age in recent years. The decline in absolute numbers of age-3 shrimp (Fig. 8) cannot be explained by changes in gear selection. The observed changes in age structure of the catch must be at least partly due to the impact of the trawl fishery.

The change in age composition of the catch is also reflected in the mean size of shrimp in the landed catch. The average number of shrimp per pound increased from 109.4 during the 1966–78 period to 118.9 for the 1979–88 period. The decline in numbers of older shrimp has been accompanied by an increase in the percentage of shrimp maturing directly into females at age-1 (Fig. 9). In recent years, levels of primary females as high as 30–50% are common. This effect has compensated for the higher cumulative harvest rates on age-2 and

Table 2

Results of exploratory regression analysis of potential factors influencing carapace length of age-1 pink shrimp. The dependent variable is an index of age-1 shrimp growth based upon mean carapace length from four selected statistical area-months.

Model	Independent variables*	Intercept	Coefficient	Adjusted r^2	P
1	U_t	–	–	–	NS
2	U_{t-1}	–	–	–	NS
3	SL_t	–	–	–	NS
4	SST_t	12.474	0.426	0.191	0.0307
5	SST_{t-1}	12.587	0.419	0.198	0.0323
6	SL_{t-1}	−20.096	0.125	0.348	0.0075
8	$CPUE_t$	17.709	−0.005	0.349	0.0018
7	$CPUE_{t-1}$	17.649	−0.005	0.287	0.006
9	Mean $CPUE_{t,t-1}$	17.877	−0.006	0.391	0.0009
10	SL_{t-1}**	−46.171	0.214	0.528	0.0009

*U = April–October upwelling from 45°N lat. 125°W long.
SL = Mean annual inverse-barometer corrected sea level at Newport, OR
SST = January–February mean sea surface temperature at Charleston, OR
CPUE = Catch-per-unit-effort for the pink shrimp fishery in statistical areas 18–28.
t = Calendar year of growth index.
**1983 sea level deleted.

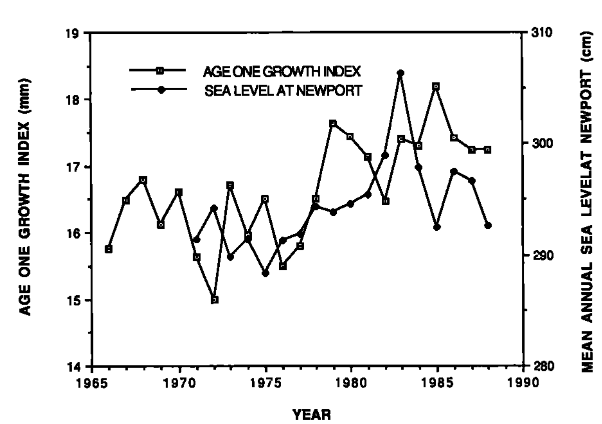

Figure 5

Age-1 growth index (mm) and mean inverse-barometer corrected sea level (cm) at Newport, Oregon for the years 1966–88 and 1971–88, respectively.

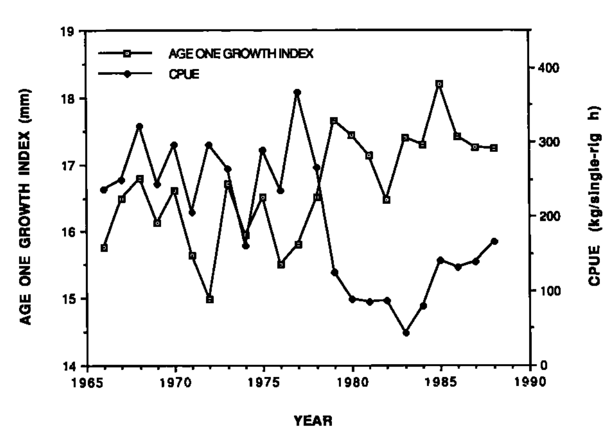

Figure 6

Age-1 growth index (mm) and pink shrimp catch-per-unit-effort (kg/single-rig equivalent hour) for 1966–88.

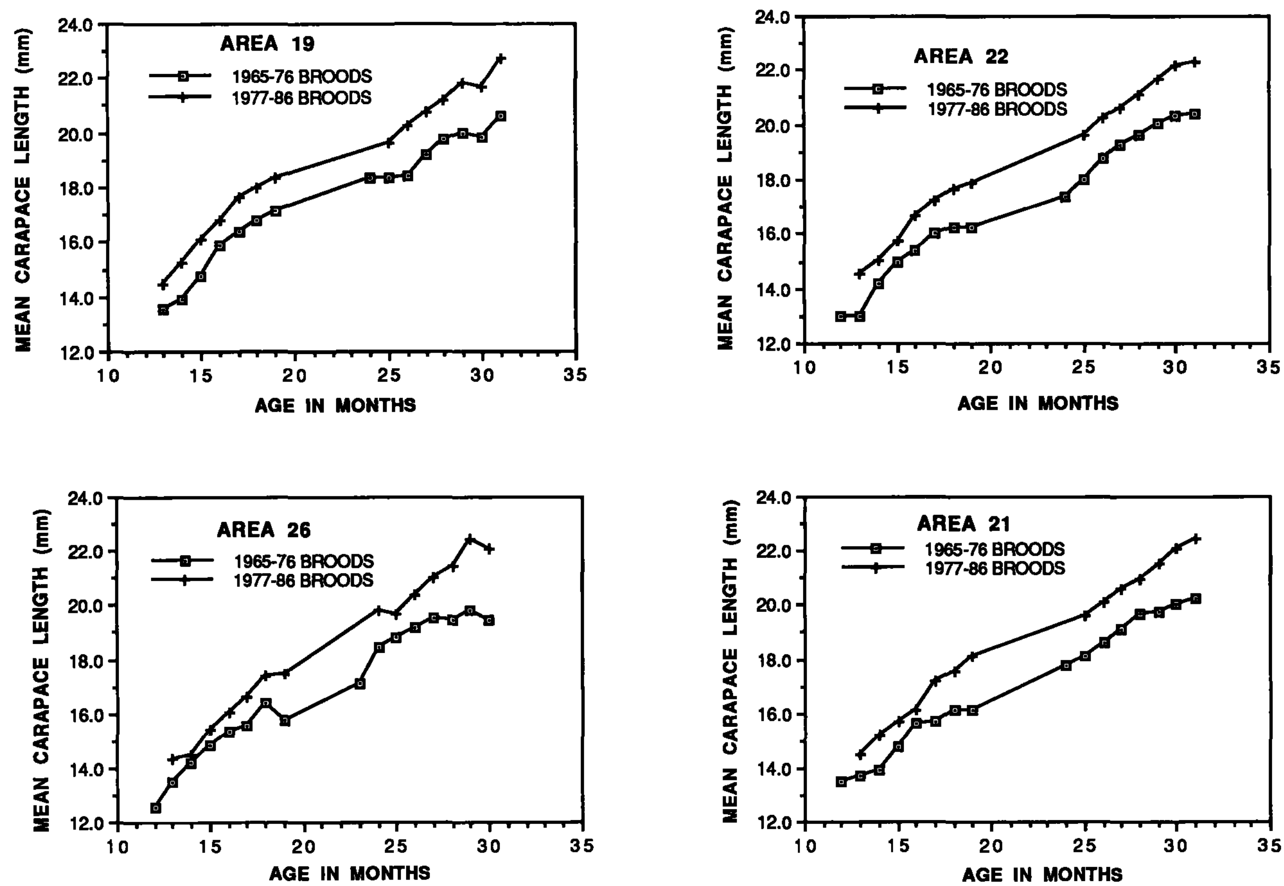

Figure 7
Mean length at age for the 1965–76 and 1977–86 broods of pink shrimp from Oregon statistical areas 19, 21, 22, and 26.

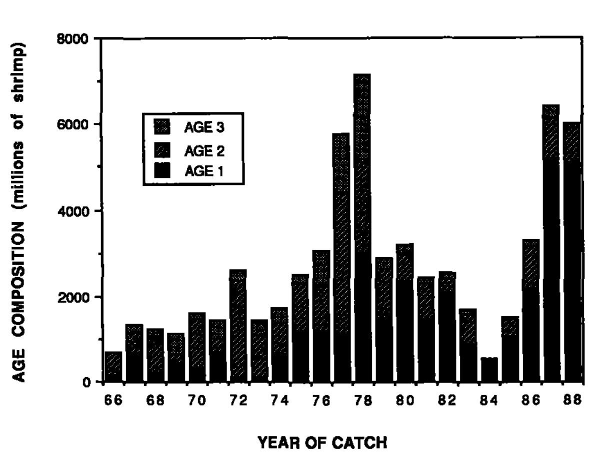

Figure 8
Age composition by number of the catch of pink shrimp from statistical areas 18–28 for the years 1966–88.

older shrimp, and a sexually balanced breeding population has been maintained (Fig. 10).

Discussion

Our analysis supports a conclusion that pink shrimp are exhibiting density-dependent growth. The transition to larger mean size at age between 1978 and 1979 coincides nearly exactly with the large drop in fishery CPUE, and the shift in age composition of the catch toward younger ages (Figs. 6, 8). This is probably due to the intensive development of the fishery during the mid 1970s (Fig. 11). The fishery continued to intensify after 1978, with subsequent effort levels falling to pre-1977 levels only in the years 1983–1985 (Fig. 12). The persistence of reduced CPUE and reduced mean age at capture are classic results of an intense size-selective harvest causing reduced levels of population biomass.

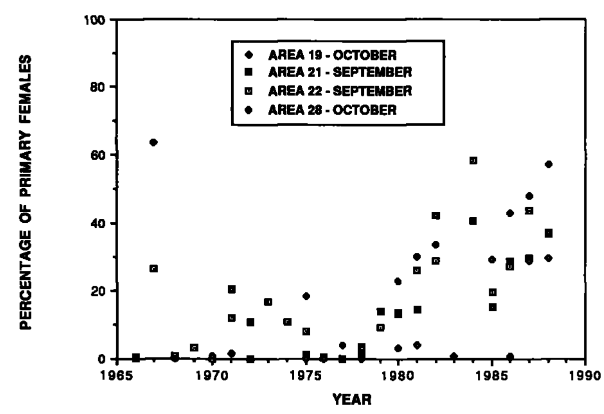

Figure 9
Percentage of age-1 pink shrimp maturing as females for four index area-months for the years 1966–88.

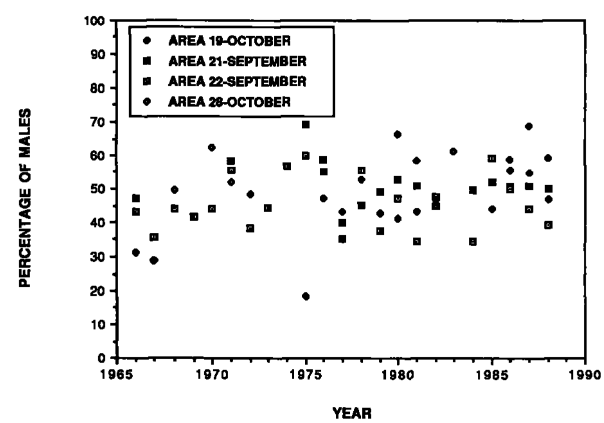

Figure 10
Percentage of male pink shrimp for four index area-months for the years 1966–88.

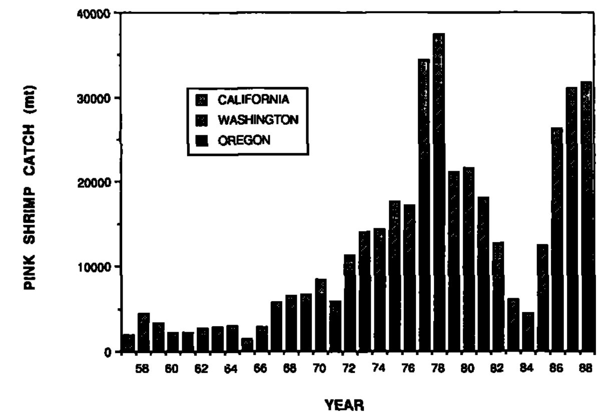

Figure 11
Combined landings of pink shrimp for the states of California, Oregon, and Washington for the years 1957–88.

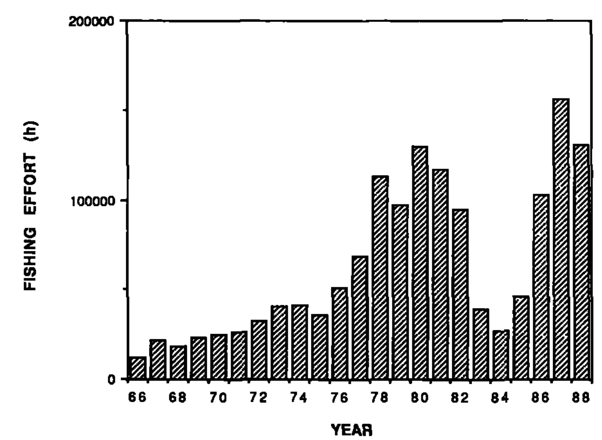

Figure 12
Fishing effort (single-rig equivalent hours) for pink shrimp in statistical areas 18–28 for the years 1966–88.

The pattern of growth in the index areas (Fig. 7) shows a slight tendency toward improved late-season growth in recent years, coincident with the season of minimum shrimp density on the grounds (Fig. 13). During the fall, age-0 shrimp begin to appear in the trawl catch in small numbers (Zirges et al. 1982). These data suggest that the improved growth occurring prior to age-13 months may be a result of decreased shrimp densities created by the trawl fishery.

The time-series of CPUE probably understates the true drop in shrimp biomass since 1978 due to the gear improvements mentioned previously. The difference in mean size at age demonstrated after 1979 may also be understated by the data shown in Figure 9. Prior to 1969 the minimum codend mesh allowed in the Oregon pink shrimp fishery was 38 mm (including one knot), while from 1969 onward codend mesh size has been unregulated (J.T. Golden, ODFW, Newport, 1981 draft). The lower curves in Figure 7, therefore, probably overestimate the mean size at age-1. Since 1979, with larger mean size, age-1 shrimp have been more completely sampled by the gear. D.R. Bernard (Oregon State Univ., Corvallis, 1983 draft) estimated that pink shrimp were fully recruited to the 38 mm mesh trawl

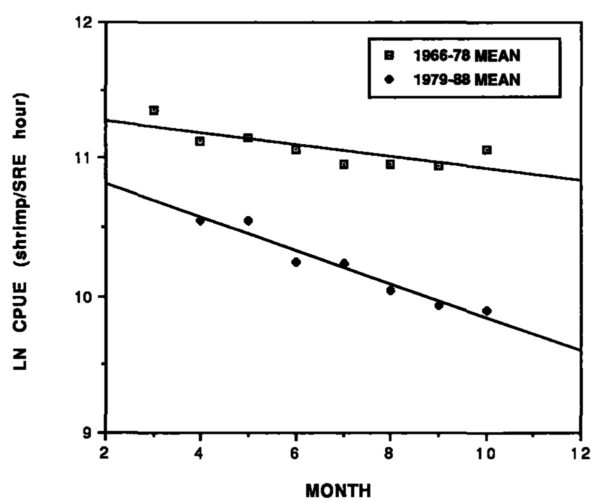

Figure 13
Log of mean catch-per-unit-effort (shrimp/single-rig equivalent hour) by month for 1966–78 and 1979–88.

at 16.6mm carapace length. Since 1979, age-1 shrimp are fully recruited to a 38mm trawl in the later months of the season and to smaller gear even sooner. In earlier years, samples were biased toward only larger age-1 shrimp, and thus, by comparison, understate the increase in growth observed since 1979.

Our exploratory correlation analysis is inconclusive in differentiating between density-dependent and environmental factors as influences on shrimp growth. While the underlying relationship between the age-1 growth index and the environmental variables tested is most likely curvilinear (Ricker 1975), the relatively narrow range of environmental variability being tested in this case warranted the simple linear approximation. The combined age-1 growth index was closely correlated with our index of shrimp density, CPUE, despite the fact that CPUE is a relatively poor index of density. We showed CPUE to be negatively correlated with mean size at age over rather large changes in CPUE. Of course, smaller changes in CPUE, not associated with major changes in population density, should be positively correlated with growth, causing CPUE to be a poor index of shrimp density. We also found adjusted sea level at Newport, Oregon in year $t-1$ to be closely correlated with the age-1 growth index, indicating that warmer bottom temperatures may have caused improved shrimp growth after 1978. Rothlisberg (1975) showed shrimp growth to be positively correlated with temperature under laboratory conditions. It is possible that elevated sea levels improve growth over the normal range observed, but at extreme levels such as occurred in 1983, the virtual complete shutdown of coastal upwelling has the reverse effect (Pearcy et al. 1985, Miller et al. 1985).

The hypothesis that sea surface or bottom temperatures (as inferred from sea level data) are controlling shrimp growth will most likely be tested over the next decade or two. In time, the relatively warm ocean conditions experienced off the Oregon coast since 1978 will probably be replaced by a colder, upwelling-dominated regime, similar to the early 1970s. The mean increase in length we have measured is equivalent to a 28% increase in average weight at age. If sea-bottom temperatures are controlling growth and return to lower levels, the drop in fishery yield will be profound. Conversely, it is unlikely that the shrimp fishery will be substantially reduced, allowing standing stocks of shrimp to rebuild to near virgin levels of the early 1970s. Thus, as we see the subsequent trend in mean carapace length at age of pink shrimp, our hypothesis of density-dependent growth will be tested further.

Charnov et al. (1981) showed that reductions in the population of age-2 and older shrimp (predominantly female) should result in increases in primary females. If Charnov is correct, the trawl fishery, through selective removal of older shrimp, should be causing this effect in the population. The result of accelerated sex change should be higher levels of primary females and a roughly stable sex ratio. Jensen (1965) and Charnov (1980) noted increased levels of young females in *Pandalus borealis* populations after intensive fishery development.

We question what these changes in population structure imply for the future productivity of the pink shrimp resource. The evidence for density-dependent growth argues for a harvest-resistant shrimp stock. Our data also support the hypothesis of Charnov et al. (1978) that the population age structure determines the age of sex change in shrimp. As a consequence of intensive harvest, the age structure has shifted toward younger shrimp. The percentage of primary females has increased, however, resulting in the maintenance of a sexually balanced breeding population. The capacity to accelerate sex change in pink shrimp also increases the stock's ability to withstand harvest pressure, by decreasing the potential for declines in larval production.

Both catch and effort levels in the pink shrimp fishery are continuing to increase. The preliminary total catch for the states of California, Oregon, and Washington is nearly 36,000 mt in 1989. The large harvests in 1987–89 (Fig. 11) appear to be the result of a combination of factors. Improved CPUE in 1987 and 1988 (Fig. 2; 1989 data unavailable) indicate some strong year classes of shrimp moving through the fishery. The total harvest levels of age-1 shrimp in these years is unprecedented in the history of the fishery. The increased size of age-1 shrimp since 1979 has made them more vulnerable to the gear and should have increased the harvest rate on age-1 shrimp relative to 1966–78. Fishing effort in the study area in 1987 and 1988 reached the two highest totals ever recorded, with 1989 likely to be as high or higher. The only other year in which effort approached levels of 1987–88 was in 1980 (Fig. 12). Postulating some improvement in vessel and gear efficiency in the years since 1980, the strong landings of 1987–89 must have been partly a result of record levels of effective fishing effort. In combination, the strong landings, high effort, and dominance of age 1 shrimp in the catch for 1987 and 1988 argue strongly for increased exploitation rates in those years. The large landings in 1989 are probably caused by the same factors.

This raises the question of what impact the increasing harvest of age-1 shrimp may have on the spawning population and subsequent recruitments. A spawner-recruit relationship has not been demonstrated for pink shrimp (Gotshall 1972). However, the Pacific Fishery Management Council (1981) identified some potential indicators of over-harvest of shrimp stocks. These included increases in the percentage of age-1 shrimp in the catch and in the percentage of primary females. In the past, reductions in age-2 and older shrimp were balanced by accelerated sex change in age-1 shrimp, and possibly by increased fecundity at age due to density-dependent growth. Levels of primary females have reached nearly 50% in some years. In such years, pink shrimp are virtually a single-age spawning stock. At some level of exploitation, accelerated sex change and density-dependent growth will not prevent declines in larval release and subsequent recruitment. The strong year-classes passing through the fishery since 1986 indicate that we've probably not reached that level of exploitation as yet.

Acknowledgments

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