Fecundity of the ocean shrimp (*Pandalus jordani*)

Robert W. Hannah, Stephen A. Jones, and Michele R. Long

Abstract: Fecundity of the ocean shrimp *Pandalus jordani* was analyzed from eight samples from the years 1989–1993 and compared with historical fecundity data for this species. Linear regressions of $\log_e$ fecundity on $\log_e$ carapace length from the 1989–1993 samples had significantly different slopes. Interannual variation in fecundity exceeded that found between areas within the same year, making it difficult to determine if the observed variation in fecundity resulted from geographic location or interannual variation. No consistent differences between the length–fecundity relationships of the recent and historical samples were demonstrated. A graphical comparison of fecundity with sea level height data provided preliminary evidence that sea bottom temperature may be influencing shrimp fecundity. Egg production, estimated from the length–fecundity relationships and from size and sex composition data from the commercial catch, showed wide variation between years and areas. Variation in sex composition explained roughly 62% of the variation in egg production. Egg production estimates, derived from a pooled length–fecundity relationship, deviated from estimates based on the individual samples by ±13–18%. These deviations were considered to be a minor source of added variance when compared with other sources of variation in the total egg production of ocean shrimp.

Résumé : La fécondité de la crevette océanique *Pandalus jordani* a été analysée à partir de huit échantillons prélevés de 1989 à 1993 et comparée à des données antérieures sur la fécondité de cette espèce. Les régressions linéaires du $\log_e$ de la fécondité par rapport au $\log_e$ de la longueur de la carapace dans les échantillons de 1989 à 1993 présentent des pentes qui diffèrent considérablement. La variation annuelle de la fécondité est plus grande que celle que l'on observe entre les diverses régions au cours de la même année; par conséquent, il est difficile de déterminer si la variation dans la fécondité est liée à l'emplacement géographique ou à la variation annuelle. Aucune différence systématique n'a été démontrée dans le rapport longueur–fécondité entre les échantillons récents et les échantillons plus anciens. Un graphique de la fécondité en fonction de la profondeur par rapport à la surface semble montrer que la température de l'eau au fond pourrait avoir une incidence sur la fécondité de ces crevettes. La production d'oeufs, estimée à partir de la relation longueur–fécondité et des données sur la composition par taille et par sexe dans les prises commerciales, varie beaucoup selon les années et les régions. La variation dans la composition par sexe explique environ 62% de la variation dans la production d'oeufs. Les estimations de la production d'oeufs, dérivées de la relation longueur–fécondité pour l'ensemble des échantillons, diverge des estimations fondées sur l'analyse des échantillons individuels par un facteur de ±13–18%. Ces écarts sont considérés comme étant une source mineure de variation supplémentaire par rapport à d'autres sources de variation dans la production totale d'oeufs de la crevette océanique. [Traduit par la Rédaction]

Introduction

Maintaining spawning stocks at adequate levels to ensure future recruitment is an important goal of fishery management. Rothschild and Fogarty (1989) and others have pointed out that stock-recruitment theory actually concerns the relationship between recruitment and egg production. Accordingly, to measure the effects of fishing on recruitment, managers need to know to what extent fishing reduces the egg production of a stock. In practice, this requires estimates of the adult spawning stock, the size and sex composition of the population, and average fecundity.

Several attempts have been made to evaluate the influence of changes in parent stock levels on subsequent recruitment in ocean shrimp (*Pandalus jordani*), without success (Abrahamson and Tomlinson 1972; Gotshall 1972; Hannah 1993). In these studies, parent stock was measured as the estimated number or biomass of female shrimp, or even more crudely, via a simple index of catch per unit effort (CPUE) in the fall just prior to spawning. These studies may have been unsuccessful because the stock indices used did not accurately reflect changes in total egg production. The principal objective of this study was to investigate the possibility of developing an index of annual egg

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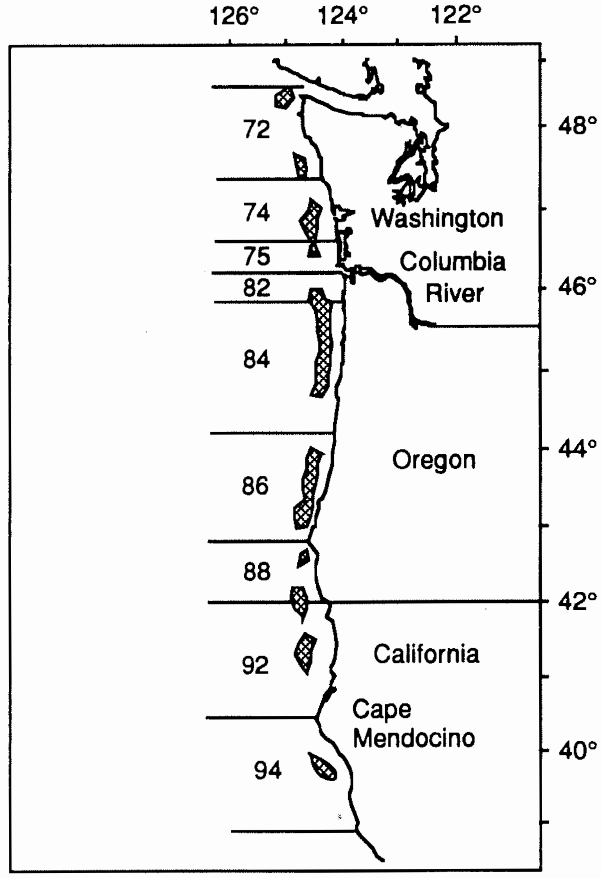
production for ocean shrimp by examining the variation found in ocean shrimp fecundity.

Dahlstrom (1970) described the fecundity of ocean shrimp from the Pacific States Marine Fisheries Commission (PSMFC) areas 92 and 94, for the year 1964 (Fig. 1). J.G. Robinson (1971, Oregon Department of Fish and Wildlife (ODFW), Newport, Oreg., unpublished data) also collected some data on the length–fecundity relationship for areas 86 and 82 for the years 1965 and 1967, respectively. However, these early data may not be suitable for estimating the fecundity of the present-day shrimp population. First, overall sample sizes were small, the largest single sample comprising only 62 shrimp, with other samples being much smaller. Second, the early samples were almost exclusively age-2 and older shrimp, while the modern day spawning population is generally composed of a large percentage of age-1 females (Hannah and Jones 1991). A third problem is that age-specific mean lengths are quite variable for ocean shrimp and have increased since the early years of the fishery (Hannah and Jones 1991). Two additional objectives of this study were to compare recent fecundity data with data from the 1960s, and to gather data to more accurately describe the average fecundity of ocean shrimp, given that age-1 females are now prevalent.

Methods

Shrimp samples were obtained opportunistically during ride-along trips on commercial shrimp trawlers. Each sample was collected on a single fishing trip, during 1 day of fishing, whenever possible. Gravid females were selected directly from each vessel's picking table or from a sample collected from the hopper. The shrimp were collected at sea, rather than from processing plants, to minimize the possibility of egg loss. Each shrimp was measured (carapace length) to the nearest 0.1 mm using vernier callipers. Shrimp were assigned to 0.5-mm length intervals by rounding downwards. For example, shrimp from 22.0 to 22.4 mm were grouped into the 22.0-mm interval. This approach was used to maintain consistency between fecundity samples and the monthly samples of fishery catch that have been collected by the ODFW since 1966. Shrimp for fecundity analysis were preserved in individual vials with 70% ethanol. Sampling of shrimp continued in this manner until a set number of shrimp from each 0.5-mm length interval had been collected. This approach was used, rather than simple random sampling, to minimize the total sample size needed to accurately depict the length–fecundity relationship of each sample. The number of shrimp collected from each size interval varied from year to year. In 1989, we collected the first five shrimp from each interval represented in the catch. In 1990 we collected the first 10 shrimp from each interval. After analyzing the 1989 and 1990 collections, we determined that collecting eight shrimp per interval should accurately depict the length–fecundity relationship, while minimizing the time spent analyzing samples. In subsequent years, eight shrimp were collected per interval. Shrimp were fixed for 24 h in 10% Formalin and then returned to 70% ethanol for storage. All eggs were carefully removed from the pleopods and counted using a dissecting scope or illuminated magnifying lens. The preservative was also strained to recover loose eggs, which were included in the total count for each specimen.

Fig. 1. Location of commercial concentrations of ocean shrimp along the U.S. Pacific coast (shaded areas) in PSMFC statistical areas 72–94.



In most years, sampling was completed during late October. However, in 1991 the fishery had slowed dramatically by October and samples were not obtained. In March 1992, prior to larval release, an opportunity to obtain fecundity samples arose during other trawl survey work and three fecundity samples were collected representing the 1991 spawning population. Data from two samples described in previous studies have also been included here for comparative purposes. The earliest sample consists of egg counts from 51 gravid shrimp collected in November, 1964, from PSMFC statistical area 92, as previously described by Dahlstrom (1970). The individual data points were digitized from Dahlstrom's (1970) Fig. 5. Dahlstrom (1970) also reported on a fecundity sample from PSMFC area 94, which was not included in this study because it is geographically distant from the collections we made off Oregon and Washington. The second sample included here consists of counts from 62 gravid shrimp collected using pots in November 1967 from PSMFC area 82. These two samples, along with fecundity data for the southern California populations of ocean shrimp, have been analyzed previously by J.G. Robinson (1971, ODFW, unpublished data).

A stepwise process was used to assess the relationship between carapace length and fecundity. First, the

Table 2. Results of linear regression analysis of $\log_e$ fecundity on $\log_e$ carapace length for samples of ocean shrimp from PSMFC areas 72–88, in the years 1989–1993, and from area 82 in 1967 (J.G. Robinson, 1971, ODFW, unpublished data) and from area 92 in 1964 (Dahlstrom 1970).

Sample	Intercept	Slope of standard regression	Intercept of GM regression	Slope of GM regression	Half width of 95% confidence interval for slope	R^2	*p* value
Present study							
Area 84, fall 1989	−2.879	3.365	−3.954	3.721	0.297	0.817	0.0001
Area 84, fall 1990	1.158	2.131	−0.306	2.597	0.296	0.672	0.0001
Area 84, spring 1992	0.282	2.374	−1.157	2.846	0.301	0.695	0.0001
Area 72, spring 1992	−1.146	2.830	−1.950	3.102	0.308	0.832	0.0001
Area 74, spring 1992	−0.805	2.714	−2.656	3.322	0.373	0.669	0.0001
Area 74, fall 1992	−2.721	3.370	−3.089	3.494	0.268	0.931	0.0001
Area 88, fall 1992	−1.051	3.002	−2.347	3.274	0.170	0.905	0.0001
Area 88, fall 1993	−1.419	3.000	−1.912	3.157	0.307	0.840	0.0001
All samples combined	−2.413	3.263	−3.493	3.616	0.109	0.821	0.0001
Prior data							
Area 82, fall 1967	−0.034	2.438	−2.447	3.235	0.545	0.568	0.0001
Area 92, fall 1964	0.213	2.393	−4.880	4.053	0.811	0.418	0.0001

Note: Slope estimates for the standard predictive and geometric mean regressions are shown along with the estimated half width of the 95% confidence interval for the slope estimates. Model is $\log_e$ (fecundity) = $a + b(\log_e$ (carapace length)). Values of R^2 and *p* refer to standard regressions only.

Fig. 6. Graphical comparison of back-transformed, fitted values (corrected for transformation bias) from geometric mean regression of $\log_e$ fecundity on $\log_e$ carapace length for samples of ocean shrimp from PSMFC areas 72–92, 1964–1993.

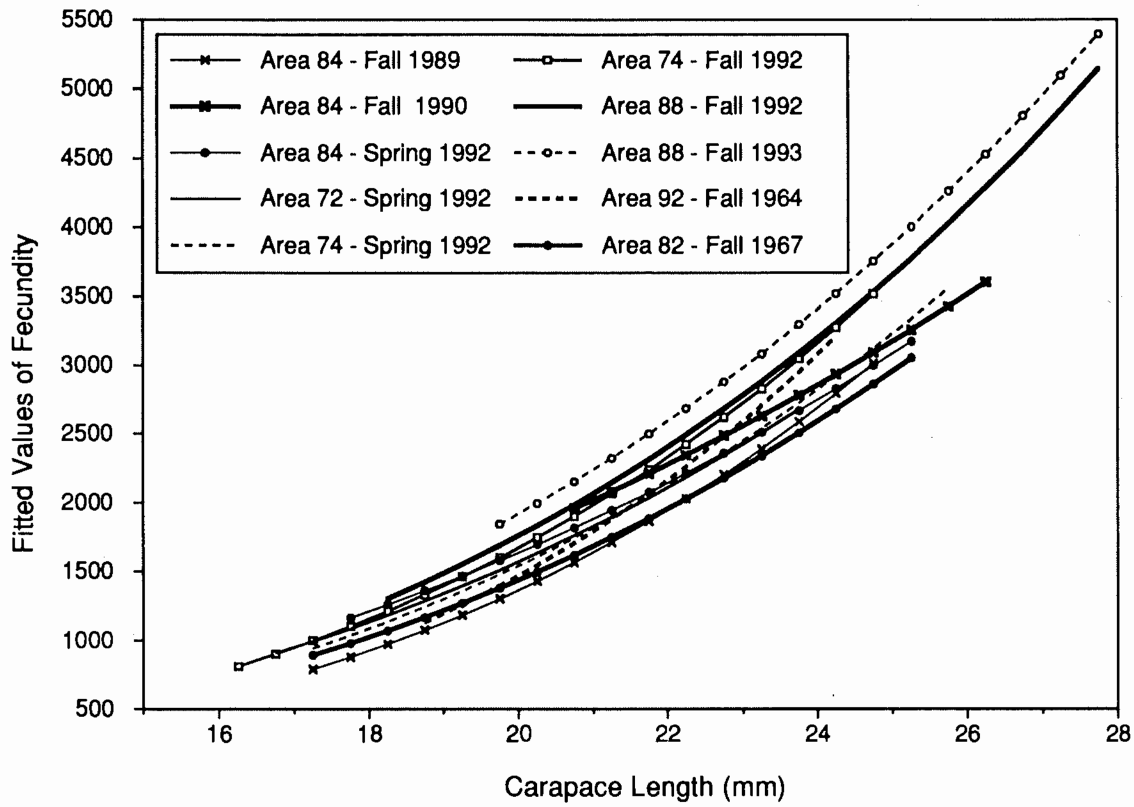


Table 3. Summary of ocean shrimp market samples used to estimate population fecundity.

Fecundity sample	Market sample	Sample size	Percent females	Percent transitionals	Age composition (%)			
					Age 0	Age 1	Age 2	Age 3+
Area 84, fall 1989	Area 84, Oct. 1989	499	25.7	0.0	0.0	80.0	19.8	0.2
Area 84, fall 1990	Area 84, Oct. 1990	301	38.9	2.0	0.0	19.6	79.4	1.0
Area 84, spring 1992	Area 84, Sept. 1991	716	30.5	7.3	0.1	85.9	8.8	5.2
Area 72, spring 1992	Area 72, Oct. 1991	263	31.2	0.8	0.3	75.6	14.4	9.7
Area 74, spring 1992	Area 74, Oct. 1991	605	40.5	0.2	1.0	88.5	3.1	7.4
Area 74, fall 1992	Area 74, Oct. 1992	202	45.0	0.0	0.0	91.1	7.9	1.0
Area 88, fall 1992	Area 88, Oct. 1992	747	57.4	6.3	0.8	94.5	4.6	0.1
Area 88, fall 1993	Area 88, Oct. 1993	436	37.8	6.2	15.8	37.2	44.2	2.8

Fig. 7. Comparison of high and low fecundity years with April–August mean sea level height at Crescent City, California. Numbers denote the year samples were collected. See Fig. 6 for high and low fecundities.

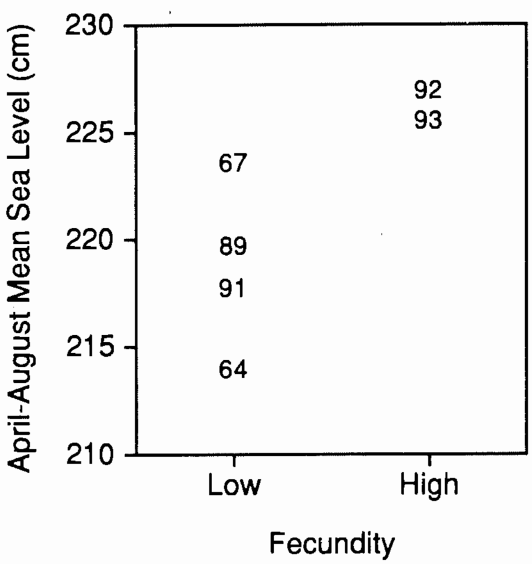
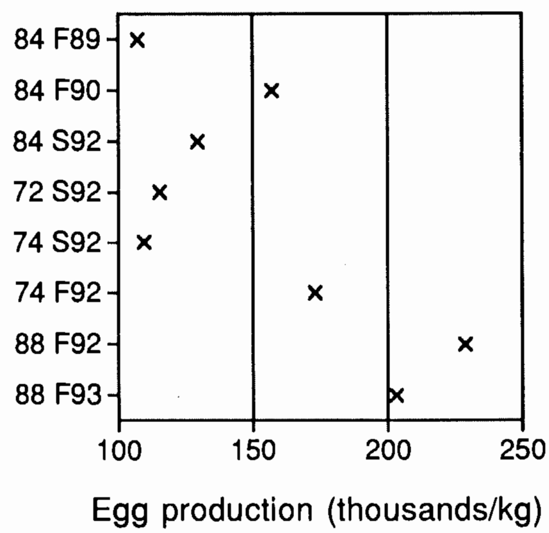


Fig. 8. Estimated ocean shrimp egg production (thousands/kg), derived from market samples (Table 3), using the length–fecundity relationships shown in Table 2. Samples are identified by statistical area followed by an S or F denoting spring or fall collection, followed by the year of collection (84 F92 denotes a sample collected from area 84 in the fall of 1992).



southernmost population showing the highest fecundity. In Teigsmark's (1983) study, the interannual variation in fecundity within an area was as great as the variation between areas in a single year, making it difficult to come to a conclusion about differences in fecundity between populations. The results of this study of ocean shrimp are consistent with Teigsmark's observations for northern shrimp. Parsons and Tucker (1986) also found significant variation in fecundity between years and areas for northern shrimp in the Northwest Atlantic; however, Apollonio et al. (1986) did not.

Egg production

The egg production estimates (Fig. 8) varied substantially, on a unit weight basis, among areas and years. The largest estimate was roughly 2.1 times the minimum estimate. High egg production was generally associated with an elevated length–fecundity curve (Fig. 6), but variation in sex composition also had a strong influence on total egg production. In a simple linear regression, the percentage of female shrimp in the market samples explained roughly 62% of the variation in egg production ($p < 0.05$), with higher percentages of females associated with increased egg production. The estimated egg production for the fall 1992 sample from area 74 was based on a market sample with 45% females (Table 3). The increased egg production for this sample resulted, in part, from higher levels of female shrimp than in most of the other samples.

The egg production estimates derived from individual samples deviated markedly from similar estimates calculated from a pooled length–fecundity relationship (Table 4). The purpose of this comparison was to measure the approximate magnitude of added variance that would be introduced by calculating historical estimates of egg production from the data collected in this study. The deviations ranged from an overestimate of 17.6% to an underestimate of 13.2%. Clearly, without a substantial annual effort to measure fecundity for ocean shrimp, it seems that the most accurate

Table 4. Comparison of estimates of population fecundity derived from ocean shrimp market sample data using two methods.

Sample	Population fecundity using method 1 (eggs/kg)	Population fecundity using method 2 (eggs/kg)	Percent difference
Area 84, fall 1989	107 270	126 201	17.6
Area 84, fall 1990	157 121	160 969	2.4
Area 84, spring 1992	129 317	133 216	3.0
Area 72, spring 1992	115 275	123 325	7.0
Area 74, spring 1992	109 517	113 312	3.5
Area 74, fall 1992	173 270	176 503	1.9
Area 88, fall 1992	228 648	206 949	−9.5
Area 88, fall 1993	203 209	176 322	−13.2

Note: Method 1 uses the length–fecundity relationship from the individual samples, while method 2 uses a length–fecundity relationship from all eight samples combined.

index of egg production that can be developed would still routinely under- or over-estimate reproductive output by 13–18%.

Deviations of this magnitude, while of some concern, may still be small in relation to other sources of variation in estimates of total annual egg production of ocean shrimp. This analysis has shown that much of the variation in egg production can be accounted for by using age-composition and sex-composition data for specific years and areas, even when using an average length–fecundity relationship. The parent stock index used by Hannah (1993), which was based on a simple average of ocean shrimp CPUE at the end of the trawl season, varied from under 50 to over 450 kg/h, a ninefold variation in density. Hannah (1995) showed that the geographic area populated by ocean shrimp in PSMFC areas 82–88 (Fig. 1) varies from roughly 81 000 to over 550 000 ha. This is roughly a sevenfold variation in stock area. Moreover, the same study linked low stock abundance with reduced geographic range and high stock abundance with expanded geographic range. In comparison, the maximum estimate of egg production from this study was roughly 2.1 times as large as the minimum estimate. Accordingly, if an index of reproductive output incorporated density (from CPUE), stock area data, and fecundity estimates based on area-specific age- and sex-composition data, it would be expected to vary broadly, with maximum values well over 10 times as large as the minimum values. With such a broad range, this type of index might still give correct information about changes in reproductive output, despite the added variance resulting from using an average length–fecundity relationship to estimate egg production. Put another way, the largest improvement in an index of reproductive output for ocean shrimp based on CPUE would likely come from incorporating the effect of changes in geographic stock area, followed by the effect of age- and sex-composition on average fecundity, followed by the effect of shifts in the length–fecundity relationship. Constructing such an index and revisiting the relationship between stock, recruitment, and the ocean environment is the next logical step in investigating the population dynamics of ocean shrimp.

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