FECUNDITY OF NORTHERN SHRIMP, PANDALUS BOREALIS, (CRUSTACEA, DECAPODA) IN AREAS OF THE NORTHWEST ATLANTIC

D. G. PARSONS AND G. E. TUCKER¹

ABSTRACT

Fecundity of the northern shrimp, *Pandalus borealis*, and relationships between number of eggs and carapace length were determined from 15 samples taken in 9 areas of the Northwest Atlantic. The sampling area extended from Davis Strait to the south coast of Newfoundland. Comparisons of samples suggested that fecundity levels can vary between seasons, years, and areas. A relationship between egg production and environmental temperature was not evident from available samples.

The northern or pink shrimp, *Pandalus borealis*, is a protandric hermaphrodite with a circumboreal distribution. In the Northwest Atlantic, it occurs from about lat. 75°N at West Greenland to about lat. 42°N at Georges Bank (Squires 1970). Fecundity of this species in the North Atlantic has been studied in southern Norway (Rasmussen 1953), northern Norway (Thomassen 1977), the North Sea (Allen 1959), Iceland (Skúladóttir et al. 1978), West Greenland (Horsted and Smidt 1956), Barents Sea (Teigsmark 1983), and Gulf of Maine (Haynes and Wigley 1969). Bottom water temperatures recorded at depths where shrimp samples were collected during these studies varied considerably between areas but were within the range of tolerance for survival of adults as reported by Allen in 1959 (-1.68° to 11.13°C).

This paper provides information on the fecundity of *P. borealis* in the Northwest Atlantic. Samples were collected in areas of known shrimp concentration off Baffin Island, in the eastern Hudson Strait and Labrador Sea, and off the south coast of Newfoundland. Bottom temperatures at sampling sites also varied between these areas but were confined to the lower half of the tolerance range (<7°C). Comparisons are made between selected combinations of the data sets presented. The possible effects of ambient temperature on fecundity levels also are considered.

MATERIALS AND METHODS

Samples of ovigerous female shrimp were col-

lected opportunistically during various research cruises conducted by or for the Department of Fisheries and Oceans, St. John's, Newfoundland, Canada, between 1971 and 1982. A total of 15 samples was selected for analysis. These were taken from the Baffin Island area (east of Cumberland Sound); Hudson Strait; North Labrador Sea; Hopedale, Cartwright, and Hawke Channels (on the Labrador Shelf); St. Mary's Bay; Fortune Bay; and the Southwest Newfoundland coast (Fig. 1). For some areas, only one sample was available while for others, samples were obtained in different months and/or different years (Table 1).

Only animals in good condition were selected from the trawl catches for the study (i.e., no noticeable damage and egg mass undisturbed). Individuals were selected over the complete size range of females, preserved in 10% Formalin² and returned to the laboratory. It was assumed that within any length group the selection (in terms of number of eggs) was random.

Oblique carapace lengths were measured to the nearest 0.1 mm using Vernier calipers. This measurement is the distance between the posterior margin of the orbit of the eye and the posterodorsal margin of the carapace (Rasmussen 1953).

All eggs were removed from the pleopods, spread in a Petrie dish, and oven dried overnight at 60°C. After drying, eggs were further separated and counted.

Accuracy of the counts was determined by recounting the eggs from 49 animals. Differences from the initial counts in 48 cases varied between -5.75%

¹Fisheries Research Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada.

²Reference to trade names does not imply endorsement by the National Marine Fisheries Service, NOAA.



Sample	Date	N	Regression equation	r ²	Temp. °C
Baffin Island	14 Aug. 1978	48	$\log_{10} F = 3.0955 \log_{10} L - 1.1417$	0.75	0.7-1.8
Hudson Strait	13 Sept. 1982	24	$\log_{10} F = 3.8880 \log_{10} L - 2.3967$	0.33	0.6
North Labrador Sea	22 Sept. 1982	43	$\log_{10} F = 3.2715 \log_{10} L - 1.4550$	0.45	0.5
Hopedale Channel	28 Sept. 1978	46	$\log_{10} F = 2.8045 \log_{10} L - 0.7202$	0.70	3.0
Hopedale Channel	11, 25 Sept. 1982	96	$\log_{10} F = 2.8884 \log_{10} L - 0.8893$	0.74	3.2
Cartwright Channel	20 Sept. 1978	45	$\log_{10} F = 3.1824 \log_{10} L - 1.3059$	0.74	3.0
Cartwright Channel	11, 26 Sept. 1982	87	$\log_{10} F = 2.5240 \log_{10} L - 0.3750$	0.68	2.0-2.4
Hawke Channel	24 Aug. 1974	20	$\log_{10} F = 3.4614 \log_{10} L - 1.6670$	0.70	_
Hawke Channel	30 Nov. 1974	-24	log ₁₀ F = 1.4613 log ₁₀ L+1.1015	0.31	2.9
Hawke Channel	23 Sept. 1975	27	$\log_{10} F = 3.0106 \log_{10} L - 1.0147$	0.68	2.7
St. Marv's Bav	18 Mar. 1971	48	$\log_{10} F = 2.3954 \log_{10} L - 0.3691$	0.53	_
St. Mary's Bay	28 Feb. 1974	44	$\log_{10} F = 2.5290 \log_{10} L - 0.5476$	0.47	_
Fortune Bay	17 Mar. 1978	48	$\log_{10} F = 3.0413 \log_{10} L - 1.1187$	0.57	1.0
Fortune Bay	30 Mar. 1979	47	$\log_{10} F = 2.6870 \log_{10} L - 0.6428$	0.70	_
SW Newfoundland Coas	t 27 Feb. 1978	48	log ₁₀ F = 2.8557 log ₁₀ L-0.7396	0.78	6.2

TABLE 1.-Regression equations for fecundity (F) vs. length (L) for Pandalus borealis in the Northwest Atlantic.

and +5.65%. The difference between the total number of eggs counted and recounted was only -0.22% of the initial count. A recount of eggs from one female indicated a difference of -9.38%. It is possible that, in this case, some of the eggs were inadvertently lost between counts.

Parameters for the relationship between number of eggs and carapace length for each sample were determined by linear regression using log-log (base 10) transformation. Some data sets were compared by analysis of covariance, assuming homoscedasticity. All statistical analyses were performed using the REG (regression) and GLM (general linear models) procedures of SAS (Statistical Analysis System).

It must be stressed that samples were obtained opportunistically and not according to a predetermined sampling design. Consequently, the statistical analyses were performed based on a practical approach rather than attempting methods for which strict sampling procedures are required. It was anticipated that differences in fecundity-length relationships could be due to seasonal, annual, and areal effects. Our data only permitted simple comparisons, investigating each factor separately.

Bottom temperatures at most sample locations were recorded to the nearest 0.1°C using either manual or expendable bathythermographs.

RESULTS

The parameters of the fecundity-carapace length relationships for all 15 samples are given in Table

FIGURE 1.—Positions of stations in the northwest Atlantic where northern shrimp fecundity samples were collected. 1. Data and the fitted line for each sample are displayed in Figure 2. Coefficients of determination ranged from 0.31 to 0.78 and all relationships were significant (differences from zero slope were highly significant). Intercepts for the log transformed data were less than zero in all but one case. Slopes ranged from 2.4 to 3.9 except for the sample with positive intercept (1.5).

Only two samples were available (Hawke Channel, August and November 1974) for comparison of fecundity between seasons. Analysis of covariance on the log of both variables indicated a highly significant difference in slopes (Table 2). The data showed that larger females (>24 mm), on average, carried more eggs in August whereas smaller females showed higher fecundity in November (Fig. 3).

Samples from specific areas and seasons were compared to determine similarities or differences between years. Five simple comparisons were possible: St. Mary's Bay - March 1971 vs. February 1974, Hawke Channel - August 1974 vs. September 1975, Fortune Bay - March 1978 vs. March 1979, Cartwright Channel - September 1978 vs. September 1982, and Hopedale Channel - September 1978 vs. September 1982.

No significant differences in either the rate of increase in fecundity with increasing size (slope) or mean number of eggs produced (intercept) were detected between years in three of the five areas compared (Table 2). These were St. Mary's Bay, 1971 and 1974; Hawke Channel, 1974 and 1975; and Fortune Bay, 1978 and 1979 (Fig. 4a, b, and c, respectively). Samples from Cartwright Channel from September 1978 and 1982 showed a significant difference in slopes at $\alpha = 0.05$ (Fig. 4d) whereas samples from the Hopedale Channel for the same



552



years were similar in slope but different in elevation (Fig. 4e). Average fecundity at length was higher in 1978 than in 1982 in the latter area.

Three comparisons were possible to detect differences between areas. In 1982, four areas were sampled during September: Hudson Strait, North Labrador Sea, Hopedale Channel, and Cartwright Channel. Analysis of the data indicated no difference in the rate of increase in fecundity with increasing size but a highly significant difference in the mean number of eggs produced (Table 2, Fig. 5a). *T*-Tests for sample means showed that the sample from Hudson Strait was different from those taken off the Labrador coast (Table 3). Fecundity in the former was less at comparable sizes.

Three areas were sampled in August and September 1978: east of Baffin Island (August), Hopedale and Cartwright Channels (September). The data from these samples also were similar in slope but different in elevations (Table 2, Fig. 5b). *T*-tests showed that the lower fecundity observed in the Cartwright Channel was significantly different ($\alpha = 0.05$) from that observed in the other two areas (Table 3).

Two samples were taken off the south coast of Newfoundland early in 1978: one from the southwest coast in February and the other from Fortune Bay in March. Eggs in both samples were "eyed", indicating late stage development. The data showed that average egg production was higher off the southwest coast over the range of sizes compared (Fig. 5c). The statistical analysis indicated similarity in slopes but a highly significant difference in elevations (Table 2).

DISCUSSION

Loss of eggs over the ovigerous period has been reported in previous studies on fecundity of P. *borealis* (Elliot 1970³; Ito 1976; Skúladóttir et al. 1978; Stickney and Perkins 1979; Stickney 1981). This loss could be incidental or due to incomplete fertilization and/or disease. Egg diameter also increases between spawning and hatching (Haynes and Wigley 1969; Ito 1976), and some eggs that are

³Elliot, D. L. 1970. Fecundity of the northern shrimp, *Pandalus borealis*. Unpubl. manuscr., 32 p. Bowdoin University, Brunswick, ME 04011.

FIGURE 2.—Number of eggs (vertical axis) vs. carapace length in mm (horizontal axis) for 15 samples of female northern shrimp taken from areas of the northwest Atlantic.

			Slopes		Intercepts	
Effect	Comparison		F-value	Prob.	F-value	Prob.
Season	Hawke Channel Hawke Channel	08/74 vs. 11/74	8.19	0.0067	_	
Year S S F F F C C C C F	St. Mary's Bay St. Mary's Bay	03/71 vs. 02/74	0.06	0.8024	0.18	0.6748
	Hawke Channel Hawke Channel	08/74 vs. 09/75	0.42	0.5215	2.30	0.1367
	Fortune Bay Fortune Bay	03/78 vs. 03/79	0.52	0.4707	1.23	0.2709
	Cartwright Channel Cartwright Channel	09/78 vs. 09/82	4.27	0.0408	0.43	0.5141
	Hopedale Channel Hopedale Channel	09/78 vs. 09/82	0.07	0.7861	26.31	0.0001
Area	Hudson Strait North Labrador Sea Hopedale Channel Cartwright Channel	09/82 vs. 09/82 vs. 09/82 vs. 09/82	1.78	0.1490	10.69	0.0001
	Baffin Island Hopedale Channel Cartwright Channel	08/78 vs. 09/78 vs. 09/78	0.49	0.6140	8.51	0.0003
	SW Newfoundland Coast Fortune Bay	02/78 vs. 03/78	0.17	0.6792	61.32	0.0001

TABLE 2.—Analyses of covariance for fecundity-length relationships.



FIGURE 3.—Comparisons of northern shrimp fecundity between seasons for the Hawke Channel, based on predicted values from equations in Table 1.

close to the periphery and loosely attached may be simply "crowded out".

The evidence of egg loss described in previous studies is sufficient to suggest that combining data from different times of year is not appropriate. The two samples compared in this study produced inconclusive results in that average fecunity was not consistently lower over the complete size range in November compared with the August sample.

Annual variation in fecundity-length relationships occurred in two of five areas sampled in different years. The rate of increase in number of eggs with

TABLE 3.—Paired comparisons for area differences when k (no. of samples) >2.

		P values for H ₀ : Mean, = mean,				
Date/sample	No.	1	2	3	4	
September 1982						
Hudson Strait	1	•				
North Labrador Sea	2	0.0002				
Hopedale Channel	3	0.0001	0.2141			
Cartwright Channel	4	0.0001	0.0695	0.4525	•	
August 1978						
Baffin Island	1	•				
Hopedale Channel	2	0.5709	•			
Cartwright Channel	3	0.0121	0.0002	•		

increasing size only differed significantly in one case, however. The reasons why fecundity differs between years are not known but could be related to changes in environmental conditions and/or egg disease (Stickney 1981). In support of the latter, it is noted that the proportion of nonviable eggs in the 1982 Hopedale Channel sample was higher than in the 1978 sample by an order of magnitude (D. G. Parsons unpubl. data). Fecundity was significantly higher in the 1978 data.

Teigsmark (1983) found that variation within a population during successive years is as great as the variation between populations in a single year and was unable to make a conclusive statement about fecundity of different populations of P. borealis in the Barents Sea. He speculated that such differences could be related to availability of food and population density.





FIGURE 4.—Comparisons of northern shrimp fecundity between years from five different areas, based on predicted values from equations in Table 1.

Based on the comparison of samples taken in 1982, it was shown that the fecunity-length relationships in three areas off Labrador were similar. Similarity was not apparent in 1978 samples which showed that fecundity in the Cartwright Channel was lower than in the Hopedale Channel. This discrepancy in results from Labrador is due to annual differences demonstrated for both channels in 1978 and 1982 samples.

The comparison by area for the 1978 data also implied similarity between the Baffin Island and Hopedale Channel samples. However, the size ranges compared were not the same. Female shrimp ranged in size from 23.7 to 34.5 for the Baffin Island sample in contrast to 21.7 to 29.0 for the Hopedale Channel sample. These differences in size likely reflect separate rates of growth and maturity in the two areas. Therefore, from a biological viewpoint, all three areas sampled in 1978 exhibited different fecundity-length relationships.

The differences between areas, described above, can be considered in relation to the temperatures present in these areas. The bottom temperature at the sampling station off the southwest coast of Newfoundland was 6.2°C, the warmest of all areas sampled (Table 1). The temperature recorded in



FIGURE 5.—Comparisons of northern shrimp fecundity between areas in 1982 and 1978, based on predicted values from equations in Table 1.

March 1978 in Fortune Bay was 1.0°C, one of the coldest areas. According to Squires (1968), the penetration of Atlantic water into the former area accounts for these warmer temperatures which persist throughout the year. In Fortune Bay, however, the deep bottom water is of mixed Atlantic and Arctic origin resulting in much colder temperatures. Thus, the lower fecundity in the Fortune Bay sample is likely linked with an overall reduction in productivity in a cold water environment. Reduced productivity has been observed previously in the cold water habitats of le Fjord du Saguenay, Quebec (Couture 1971) and the Barents Sea (Berenboim 1982).

The sample taken east of Baffin Island showed relatively high fecundity in cold water $(0.7^{\circ}-1.8^{\circ}C)$ compared with other cold water areas. Also, average size of females was larger than encountered elsewhere with largest females carrying clutches in excess of 4,300 eggs. This is similar to a situation in the Sea of Japan where female shrimp carried similar numbers of eggs as those (at comparable lengths) off Labrador. Again, greater sizes were attained and egg counts as high as 4,900 were encountered (Ito 1976). Growth and maturation are delayed in colder water (Allen 1959; Rasmussen 1969; Butler 1971) and shrimp in these two cold water environments likely live longer than conspecifics on the Labrador Shelf.

Dupouy et al. (1981) concluded that shrimp off Baffin Island spawned intermittently based on the high proportion of nonspawning females observed during a survey in 1979. If all females do not spawn annually, more time is available for growth. (Ovigerous females do not molt.) This can account for the larger sizes attained in the colder area. Failure to spawn annually reduces reproductive potential but is compensated to some degree by the large sizes females attain (larger females carry more eggs) and the apparently increased longevity.

Samples taken in 1982 in the Hudson Strait and North Labrador Sea came from waters of 0.6° and 0.5°C, respectively, but only data from the former were significantly different ($\alpha = 0.05$) from samples taken in the warmer Hopedale and Cartwright Channels. Data from Haynes and Wigley (1969) showed higher fecundity in warmer water ($\sim 5^{\circ}$ C) of the Gulf of Maine where a 28 mm female can proPARSONS and TUCKER: FECUNDITY OF NORTHERN SHRIMP

duce around 2,800 eggs compared with 1,900-2,000 in the Cartwright Channel (2°-3°C). In the Gulf of St. Lawrence, temperatures were similar to those in the Gulf of Maine but fecundity in 1970 (E. J. Sandeman⁴ unpubl. data) was comparable with levels observed in the colder Labrador channels. Allen (1959) reported smaller shrimp and fewer eggs for *P. borealis* in the North Sea (~9°C) compared with the colder area off Southern Norway (7°C).

CONCLUSIONS

Fecundity of *Pandalus borealis* in the areas of the Northwest Atlantic considered in this study was generally lower than observed previously in the Gulf of Maine (Haynes and Wigley 1969) and off Southern Norway (Rasmussen 1953). Fecundity can vary seasonally, annually, and between areas, making conclusions based on such data difficult. Skúladóttir et al. (1978) concluded that fecundity does not seem to be a useful characteristic for distinguishing between populations unless it is certain that no egg loss or hatching has taken place. The results of the present study concur with these findings and those of Teigsmark (1983) which also showed that annual variation within areas also must be considered.

In some comparisons between areas, there appears to be reduced egg production in areas with low environmental temperature. In others, this is not at all apparent, especially at extremely cold and warm temperatures. Thus, there is no clear relationship between fecundity and environmental temperature, especially at the extremes of the range of temperature tolerance.

Squires (1968) described warm water areas as areas of high reproductive potential for shrimp and colder regions as areas of low reproductive potential. The cold water bays of Newfoundland and the eastern Hudson Strait fit into the latter category in terms of shrimp fecundity. Other cold water concentrations of shrimp appear to be better adapted such as those off Baffin Island, in the North Labrador Sea and Sea of Japan. In these cases, environmental conditions other than temperature (e.g., availability of nutrients) may be more important.

ACKNOWLEDGMENTS

We are grateful to the many technicians and

casual employees who assisted in collecting the data over the years and performed the laborious task of counting the eggs. In this regard, the services of W. Edison are particularly appreciated. Assistance in the statistical analyses was provided by D. Stansbury.

LITERATURE CITED

Allen, J. A.

1959. On the biology of *Pandalus borealis* Krøyer, with reference to a population off the Northumberland coast. J. Mar. Biol. Assoc. U.K. 38:189-220.

BERENBOIM, B. I.

1982. Reproduction of the shrimp Pandalus borealis populations in the Barents Sea. Okeanologiya 22(1):118-124.

BUTLER, T. H.

1971. A review of the biology of the pink shrimp, Pandalus borealis Krøyer 1838. Can. Fish. Rep. 17:17-24.

COUTURE, R.

1970. Reproduction de *Paudalus borealis* Krøyer (Crustacea, Decapoda) dans le fjord du Saguenay. Nat. Can. 97:825-826.

DUPOUY, H., C. LEROY, AND J. FRÉCHETTE.

1981. Étude des Stocks de Crevette Pandalus borealis du Détroit de Davis. Sci. Pêche, Bull. Inst. Pêches Marit. 311, mars 1981, 21 p.

HAYNES, E. B., AND A. L. WIGLEY.

1969. Biology of the northern shrimp *Pandalus borealis* in the Gulf of Maine. Trans. Am. Fish. Soc. 98:60-76.

HORSTED, SV. AA., AND E. SMIDT.

1956. The deep sea prawn (*Pandalus borealis* Kr.) in Greenland waters. Meddelelser fra Danmarks Fiskeri-og Havundersøgelser. Ny Serie, Bind I, Nr. 11, 118 p.

1976. Some findings concerning *Pandalus borealis* Krøyer originating in the Sea of Japan. Bull. Jpn. Sea Reg. Fish. Res. Lab. 27, p. 75-89.

Rasmussen, B.

1953. On the geographical variation in growth and sexual development of the deep sea prawn (*Pandalus borealis* Kr.). Norweg. Fish. Mar. Invest. Rep. 10(3):1-160.

1969. Variations in protandric hermaphroditism of *Pandalus* borealis. FAO Fish. Rep. 57:1101-1106.

SKÚLADÓTTIR, U., E. JÓNSSON, AND I. HALLGRÍMSSON.

1978. Testing for heterogeneity of *Paudalus borealis* populations at Iceland. ICES C.M. Doc. 1978/K:27, 41 p. SQUIRES, H. J.

QUIRES, H. J.

- 1968. Relation of temperature to growth and self-propagation of *Pandalus borealis* in Newfoundland. FAO Fish. Rep. 57:243-250.
- 1970. Decapod crustaceans of Newfoundland, Labrador and the Eastern Canadian Arctic. Fish. Res. Board Can., Manuscr. Rep. Ser. No. 810, 212 p.

STICKNEY, A. P.

1981. Laboratory studies on the development and survival of *Pandalus borealis* eggs in the Gulf of Maine. *In* T. Frady (editor), Proceedings of the International Pandalid Shrimp Symposium, Kodiak, Alaska, 1979, p. 395-406. Sea Grant Rep. 81-3.

STICKNEY, A. P., AND H. C. PERKINS.

1979. Environmental physiology of northern shrimp, *Pandalus borealis*. Completion Report. Maine Dep. Mar. Res., Proj. 3-277-R, 66 p.

⁴E. J. Sandeman, Fisheries Research Branch, Department of Fisheries and Oceans, P.O. Box 5667, St. John's, Newfoundland A1C 5X1, Canada.

Іто, Н.

TEIGSMARK, G.

1983. Populations of the deep-sea shrimp (*Pandalus borealis* Krøyer) in the Barents Sea. Fiskeridir. Skr. Serv. Havunders. 17:377-430. THOMASSEN, T.

1977. Comparisons of growth, fecundity and mortality between two populations of *Pandalus borealis* in Northern Norway. ICES C.M. Doc. 1977/K:38, 16 p.