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A Comparison of the Growth of Northern Shrimp (*Pandalus borealis*) from Four Regions of the Northwest Atlantic

by

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INTRODUCTION

In 1981, the Northwest Atlantic Fisheries Organization (NAFO) convened an ageing workshop on northern shrimp (Pandalus borealis) to address the numerous problems encountered when studying growth in the species. The report of this workshop (Fréchette and Parsons, 1983) summarized the results achieved during the two sessions and provided recommendations for future research in this area. Since then, research on shrimp by Science Branch in the Newfoundland Region has focused on determining growth patterns of the species in various areas of the Northwest Atlantic where commercial fisheries occur.

The interpretation of growth in P. borealis (hereafter referred to simply as shrimp) is based on the assumption that modes occuring in length frequency distributions represent year-classes. This assumption is tenuous in that modes are frequently severely overlapped and that more than one age group may be contained within a single normal component. However, for many stocks in the more northern waters of the northwest Atlantic, ontogeny appears to be synchronous within year classes. Sex change occurs at a specific age and the occurrence of primary females (Jägersten, 1936) has not been observed. Thus, it is felt that separation of length distributions for these shrimp is an acceptable method of estimating age composition, recognizing that the largest mode of multiparous females is composed of more than one year class.

The first descriptions of shrimp growth followed Peterson's (1891) method which traced the displacement of various size groups over time (Berkeley, 1930; Hjort and Ruud, 1938; Allen, 1959; Haynes and Wigely, 1969). More recently, age composition of samples has been determined by modal anlysis of distribution mixtures using both graphical (e.g. Cassie, 1950, 1954; Tanaka, 1962) and analytical (e.g. Abramson, 1971; Macdonald and Pitcher, 1979) methods.

A detailed description of shrimp growth for populations in the Barents Sea based on modal analysis was given by Teigsmark (1983). Parsons et al. (1986) combined studies on larval growth, observations on the sizes of shrimp from the stomachs of cod (Gadus morhua) and modal analysis of shrimp length frequencies from survey data to determine age and growth in an area off northeastern Newfoundland and southern Labrador. Both these recent studies employed analytical methods of modal separation. All the above attempts at ageing, however, have not considered the moulting frequency involved with increases in size. Although growth per moult has been studied extensively for larval and early juvenile stages (Stickney and Perkins, 1977; Haynes, 1979; Wienberg, 1982; Nunes, 1984), virtually no data are available on the number of moults which adults undergo annually. Therefore, the models chosen to describe growth in this species have ignored the step-wise increase in the size of the animals and defaulted, primarily, to the von Bertalanffy (1938) growth equation (Fréchette and Parsons, 1983).

This paper examines sampling data from four areas of the northwest Atlantic, interprets age and growth for each and compares the results obtained between areas and with previous findings in the literature. Discussion is also included on the problems of statistical comparison and the choice of an appropriate growth model.

METHODS AND MATERIALS

Random samples of shrimp were collected during research surveys conducted by the Department of Fisheries and Oceans in the northwest Atlantic from 1978 to 1987. Although a number of different research vessels were used over this period, the sampling gear, a Sputnik 1600 shrimp trawl, remained constant. Mesh size ranged from about 80 mm in the wings to 42 mm in the cod-end and the last 6 m of codend were lined with 13-mm mesh to prevent the loss of smaller animals. The trawl was towed routinely at 6.5 km per hour for 0.5 hours. Samples were preserved in 10% formalin for subsequent observation at the laboratory.

Pooling of samples within year was done for areas separately after the initial examination of the data revealed no substantial differences in the overall length distributions (i.e. similar size range, similar modes). Data were analysed for four areas: St. Anthony Basin - NAFO Division 3K (5 samples, 1981-86); Cartwright Channel - Div. 2J (8 samples, 1980-87); Hopedale Channel - Div. 2H (7 samples, 1981-87); Davis Strait - Subareas 0+1 (6 samples, 1978-86). Samples from Davis Strait for 1980, 1981 and 1984 were obtained from commercial vessels which also use gear with a codend mesh size of about 40 mm but do not use a liner. The general locations of the four sampling areas are shown in Figure 1.

Oblique carapace lengths (Rasmussen, 1953) were measured to the nearest 0.1 mm using Vernier calipers and subsequently combined to 0.5 mm. Shrimp were separated into male and female components based on the characteristics of the endopod of the first pleopod (Rasmussen, 1953). Females were further separated into primiparous (first time spawners) and multiparous (spawned previously) groups based on the condition of the sternal spines (McCrary, 1971).

Modal analyses (Macdonald and Pitcher, 1979) were performed on male length distributions only, to obtain estimates of the mean for each normal component. Mean sizes of primiparous and multiparous females were calculated directly from the sampling data. In doing so, it was assumed that primiparous females constitute a separate age class and that multiparous females comprise a number of age classes. The validity of these assumptions is discussed in more detail below. Ageing of the various components was based on the findings of Parsons et al. (1986) and assumes that growth rates of shrimp larvae are similar throughout the sampling area.

To maintain objectivity in the interpretation of the age composition of the samples, preliminary modal analyses were conducted by area for each year, separately. The results, in terms of mean size at age, were tabulated and reviewed for consistency between years. Then, a final analysis was conducted by area for all years combined. It was felt that this method provided the most appropriate description of average growth within each area by inherently averageing out year to year variability in length at age as well as variation in the growth rates of the different cohorts. Comparison of the growth rates by area was descriptive only, as there appears to be no suitable statistical procedure for the analysis of such data.

RESULTS

Five years of sampling data from the St. Anthony Basin revealed four modes of male shrimp that were interpreted as year classes (Fig. 2, Table 1). Although three or four modes were evident in most years, severe overlap in many cases made it difficult to estimate the parameters of some components. Only the means estimated with some confidence are given in Table 1 (i.e. those with large standard errors were not used). For 1986, average length was used for males, as well as primiparous and multiparous females, there being only one clear mode in the length frequency. Estimated mean lengths for each presumed year class were close, especially for the younger ages and there was no overlap in the range of means with adjacent year classes. Female groups were well separated by over 1 mm carapace length (cl) and clearly separated from the largest group of males. These preliminary analyses were intended to reveal consistencies in the data between years in terms of the number of age groups present in the samples. Although the final "averages" are not clearly represented in all the samples, there is evidence to suggest that they occur with some regularity from year to year.

Samples from Cartwright Channel from 1980 to 1987 provided evidence of five modal groups of male shrimp, compared to four in the previous area. It is noted, however, that means for five components could not be estimated from any sample in any single year (Table 2). Individual length frequencies (Fig. 2) show that modes were severely overlapped, especially between the second and third and the fourth and fifth components. In samples where a fifth mode was not obvious (1984 and 1986), the mean size of the fourth tended to be substantially larger. Similarly, the mean sizes of other normal components could have been either over or underestimated, depending on whether or not the overlap had been resolved. A detailed review of length frequency data from surveys revealed that over a wide range of depths, the five "average" size groups evident here were apparent (Parsons, unpublished). Despite these problems, the range of the mean lengths estimated did not overlap adjacent year class estimates. Primiparous females were over 2 mm cl larger than the largest male component in most cases and, similarly, the multiparous females were larger than the primiparous group. Although only a single mean length was estimated for the oldest females, it was quite evident that the distributions comprise more than one component.

Again, five modes of male shrimp were evident in samples from the Hopedale Channel (Fig. 2, Table 3). As many as four were estimated in samples from two years, but in one case (1981) no solution was achieved. Also, the smallest modal group at 13 mm was clearly evident in only one sample (1982). As in Cartwright Channel, modes were overlapped, especially the second and third and the third and fourth components. The "average" lengths were similar to those obtained for Cartwright and the associated ranges did not overlap with those of the adjacent year classes. The difference between average lengths of the female groups was less than 2 mm for all years except 1983 and the distributions suggested that the multiparous group consisted primarily of one component.

There was evidence of six modes of male shrimp from the Davis Strait (Fig. 2, Table 4). All six were apparent in the 1978 sample and five in 1979, while the smallest three modes were poorly represented in the last three years. The extra mode observed in this area represents an age class which appears to be one year younger than the smallest mode present in the other areas. The mean lengths of the three largest male groups were substantially greater than the corresponding means in the more southerly areas, as were the mean sizes of the two female groups. Length distributions for the multiparous females indicated the presence of more than one component, similar to that observed in Cartwright Channel. In fact, even the primiparous group exhibited bimodality in some of the samples analysed.

Based on these preliminary observations and analyses, estimates of the average lengths at assumed ages and the number of male components were used in a final modal analysis by area for all years combined (Fig. 3). For female groups, the average lengths were calculated from the pooled data set. Results of the modal analyses are summarized in Table 5. For the St. Anthony Basin, the procedure would not run freely (i.e. constraints needed for parameters) but acceptable standard errors were obtained by holding the standard deviation of the largest component fixed at a previously estimated value (1.20). Assuming four modes and mean lengths as estimated in the preliminary analyses, the expected distribution was not significantly different from the observed (chi-square = 14.3, P = 0.51) (Fig. 4). The extreme overlap of the pooled Cartwright Channel data was very difficult to resolve. The "best" run was obtained by holding the proportions and standard deviations of the third and fourth modes fixed at previously estimated values. Under these numerous assumptions, the expected distribution was not significantly different from the observed (chi-square = 13.8, P = 0.61). The combined data for Hopedale Channel provided more information on the left side of the length frequency distribution and another size group with average length of 7.7 mm cl became evident (Fig. 3). Modal analysis of the larger sizes based on the preliminary findings was achieved by holding the standard deviations of the second, third and fourth modes fixed at previously estimated values. However, the overall fit was not as good as in the other two cases (chi-square = 21.8, P = 0.19). The analysis for Davis Strait ran freely assuming six components and using the means estimated previously. The observed and expected frequencies were similar (chi-square = 25.1, P = 0.24). Five of the six means estimated in the final run were close to the initial starting values but the second was about 2 mm smaller. In reviewing the yearly data, it was observed that this second mode was only obvious in the 1978 sample. Therefore, the mean size of this group was set at 11.9 mm cl as estimated from that sample.

Ages were assigned for each area assuming the smallest size group at roughly 8 mm cl represented one-year-olds (Parsons et al., 1986). The results, summarized by area (Table 6), show the apparent differences in growth and maturation (Fig. 5). Shrimp in the St. Anthony Basin function as males up to age 5 then change sex and function first as females at age 6. In the more northern areas, growth rate is slower and sex change occurs between ages 6 and 7. Growth appears to be similar in the Cartwright and Hopedale Channels except that, in the former, estimated mean length at age is slightly smaller in most cases. Although maturation in Davis Strait appears similar to that in the Channels, growth rate appears greater and, beyond age 3, mean length at age is substantially larger.

DISCUSSION

The above results indicate variation in the rates of both growth and maturity for shrimp stocks in the northwest Atlantic. First spawning as females occurred at age 6 in the St. Anthony Basin and at age 7 in the areas farther north. Teigsmark (1983) also noted first spawning at age 6 in a Barents sea population, but thereafter spawning occurred every second year. This differs from the stocks studied here in that annual spawning occurs for the majority of females. Parsons et al. (1986) interpreted data collected in 1984 from the St. Anthony Basin to suggest that first spawning as females occurred at age 5. It now appears that the size groups in that sample were severely overlapped and that the number of ages was underestimated. The methodology used here reduces the possibility of misinterpretation by looking for consistency in the occurence of size groups over time.

The similarity between observations in the Hopedale and Cartwright Channels might be expected, given that environmental conditions in the two areas are similar. The smaller mean lengths at several ages in the latter are consistent with the slightly colder water temperatures that have been observed in this Channel (Parsons, 1982). Temperatures in the St. Anthony Basin where shrimp were highly concentrated ranged from approximately 2 to 4 °C, similar to the range found in the channels to the north. The accepted philosophy is that both growth and maturity are delayed in colder waters and longevity increases (Allen, 1959; Haynes and Wigley, 1969; Rasmussen, 1969; Butler, 1971). However, from the data examined here, the differences between the St. Anthony Basin stock and those found farther north cannot be explained in terms of environmental temperatures.

Although the range of bottom temperatures in Davis Strait where shrimp occur (1 to 4 °C) (Atkinson et al., 1982) is similar to that off Labrador,the mean lengths at age are considerably larger beyond age 3. It is possible that the modes in the length frequencies are sufficiently overlapped to obscure another year class. If this were the case, then a trend of slower growth and increased longevity with increasing latitude would be more firmly established. Length frequencies for 1979 and 1981 from this area suggest the possibility that an additional mode exists at roughly 16.5 mm, between the adjacent modes at 15 and 18 mm. Before a definitive statement can be made about growth and maturity in this area, more samples for a longer period and covering a larger area must be analysed.

The results described here for Davis Strait differ greatly from those reported previously by Horsted and Smidt (1956). For some shrimp stocks in near and inshore areas, first spawning as females was thought to occur at ages 4 or 5. The first female age class in Disko Bay, where the bottom temperatures appear to be colder than on the Davis Strait grounds, was estimated to be 5 years old compared to 7 (possibly 8) in the offshore areas interpreted in the present study. Although the interpretations of age are not in agreement, it is interesting to note that Horsted and Smidt (1956) also observed slower rates of development with increasing latitude which could not be associated with changes in temperature.

Indications of bimodality in the primiparous female group for the Davis Strait samples introduces another problem in the interpretation of age for this stock. For other stocks considered in this study, it appears that sex change occurs at a specific age, and the oldest age class of males is easily separated from the youngest female group. However, it has been observed that for some populations, two modal length groups of transitionals may exist, simultaneously (Rasmussen, 1953; 1969), indicating that sex change may occur within more than one year class. If this occurs in the Davis Strait, then the mean sizes at ages 6 and 7 might be underestimated, depending on the proper assignment of age to first "mode" of primiparous females. Again, samples from this area need to be examined in detail to determine whether or not sex change occurs at a specific age. For certain areas at west Greenland, Horsted and Smidt (1956) have already observed "Type B" development in which a fraction of 4(?) year olds continues to function as males until age 5(?) while the remainder changes sex.

The comparison of growth between areas presented here is descriptive only. There does not appear to be any conventional statistical procedure to test for similarities among stocks using the data as calculated in this type of analysis. Misra (1987) provided a program to compare statistically several von Bertalanffy growth curves, but such curves are generally derived from a number of observations of length at age. The data generated from modal analysis does not appear to be suitable for such treatment. Indeed, though the von Bertalanffy model has been used in the past to provide a general description of shrimp growth (Fréchette and Parsons, 1983), it is not efficient even for that purpose. Not only does it preclude the stepwise increments characteristic of crustacean growth, but as well ignores the rapid growth that occurs during the transitional period. There is a real need to develope appropriate models and statistical analyses so that interpretations such as those made in this study can be supported (or rejected) within the limitations of the data.

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Table 1. Mean carapace lengths (mm) estimated by modal analysis for male shrimp and by direct calculation for primiparous and multiparous females in the St.Anthony Basin.

	MALES				FEMALES	
YEAR	I	II	III	IV	PRIMI	MULTI
1981	13.4			20.4	22.9	24.2
1983	13.4	16.1	17.9	19.9	22.6	24.8
1984		16.2		19.2	22.7	23.9
1985		16.6	18.6	20.3	21.9*	23.9
1986		16.1			22.4*	23.6
AVERAGE	13.4	16.3	18.3	20.0	22.7	24.1

* Sample size too small for inclusion in average.

Table 2. Mean carapace lengths (mm) estimated by modal analysis for male shrimp and by direct calculation for primiparous and multiparous females in the Cartwright Channel.

	MALES					FEMALES	
YEAR	I	II	III	IV	V	PRIMI	MULTI
1980		15.3		19.1	20.7	22.9	24.6
1981	12.0			18.6	20.7	23.3	25.1
1982				19.0	20.6	23.2	24.6
1983		14.8			20.4	22.6	25.3
1984		15.2	17.7	19.8		21.9	24.1
1985			17.4	19.1	20.7	22.1	24.3
1986	12.3	15.0	17.7	19.6		20.7*	24.0
1987					20.5	23.9	25.4
AVERAGE	12.2	15.1	17.6	19.2	20.6	22.8	24.7

* Sample size too small for inclusion in average.

Table 3. Mean carapace lengths (mm) estimated by modal analysis for male shrimp and by direct calculation for primiparous and multiparous females in the Hopedale Channel.

	MALES					FEMALES	
YEAR	I	II	III	IV	V	PRIMI	MULTI
1981						23.9	24.7
1982	13.0	15.6		19.0	21.2	24.3	25.3
1983			17.8	19.4		22.8	25.0
1984		15.6	17.5	19.1	20.5	22.5	24.3
1985				19.1	20.8	22.7	24.0
1986			17.7	19.4	21.1	23.5	24.5
1987			16.9	18.7	20.9	23.9	25.1
AVERAGE	13.0	15.6	17.5	19.1	20.9	23.4	24.7

Table 4. Mean carapace lengths (mm) estimated by modal analysis for male shrimp and by direct calculation for primiparous and multiparous females in the Davis Strait.

	MALES						FEMALES	
YEAR	I	II	III	IV	V	VI	PRIMI	MULTI
1978	7.8	11.9	15.2	18.4	20.3	22.7	25.4	26.5
1979	9.3		14.8	18.5	20.3	22.6	25.0	26.4
1980			14.5		19.9	22.6	25.8	26.5
1981				17.9	21.1	23.5	25.2	26.4
1984				18.3	20.3	22.0	24.3*	25.7
1986				18.4	20.7	22.3	24.9	25.6
AVERAGE	8.6	11.9	14.8	18.3	20.4	22.6	25.3	26.2

* Sample size too small for inclusion in average.

Table 5. Results of Macdonald and Pitcher (1979) modal analyses by stock area, all years combined. CL = carapace length, S.D. = standard deviation, S.E. = standard error.

STOCK AREA	MODE	%	(S.E.)	MEAN CL	(S.E.)	S.D.	(S.E.)
ST.ANTHONY BASIN	1	11.0	(7.6)	13.4	(0.8)	1.13	(0.27)
	2	47.1	(17.0)	16.2	(0.2)	1.18	(0.36)
	3	22.3	(16.6)	18.7	(0.3)	0.89	(0.29)
	4	20.0	(8.7)	20.0	(0.3)	1.20	(*)
CARTWRIGHT CHANNEL	1	1.8	(0.9)	12.3	(0.4)	0.82	(0.22)
	2	20.3	(7.6)	15.5	(0.4)	1.19	(0.29)
	3	35.6	(*)	18.0	(0.4)	1.19	(*)
	4	17.0	(*)	19.1	(0.4)	1.17	(*)
	5	25.3	(6.9)	20.5	(0.2)	1.01	(0.08)
HOPEDALE CHANNEL	1	6.5	(3.1)	13.3	(0.6)	1.28	(0.22)
	2	21.4	(2.0)	15.5	(0.2)	1.08	(*)
	3	16.0	(6.1)	17.4	(0.3)	0.88	(*)
	4	27.7	(5.6)	19.0	(0.7)	1.13	(*)
	5	28.4	(1.1)	20.9	(0.4)	1.14	(0.11)
DAVIS STRAIT	1	0.6	(0.5)	7.9	(0.2)	0.21	(0.38)
	2	2.2	(1.0)	10.0	(0.4)	1.36	(0.69)
	3	10.4	(2.0)	15.5	(0.3)	1.84	(0.43)
	4	7.2	(3.9)	18.3	(0.2)	0.52	(0.14)
	5	29.2	(19.9)	20.3	(0.3)	0.97	(0.33)
	6	50.4	(17.3)	22.3	(0.4)	1.23	(0.14)

* = Parameters constrained at previously estimated values.

Table 6. Mean carapace length (mm) at age by stock area as determined through modal analysis of males and separation of primiparous and multiparous females by sternal spines (all years combined).

	ASSUMED AGE (YEARS)							
STOCK AREA	1	2	3	4	5	6	7(+)	8+
ST.ANTHONY BASIN		13.4	16.2	18.7	20.0	22.6	24.2	
CARTWRIGHT CHANNEL		12.3	15.5	18.0	19.1	20.5	22.8	24.7
HOPEDALE CHANNEL	7.7	13.3	15.5	17.4	19.0	20.9	23.4	24.8
DAVIS STRAIT	7.9	11.9*	15.5	18.3	20.3	22.3	25.4	26.1

* From 1978 sample only.

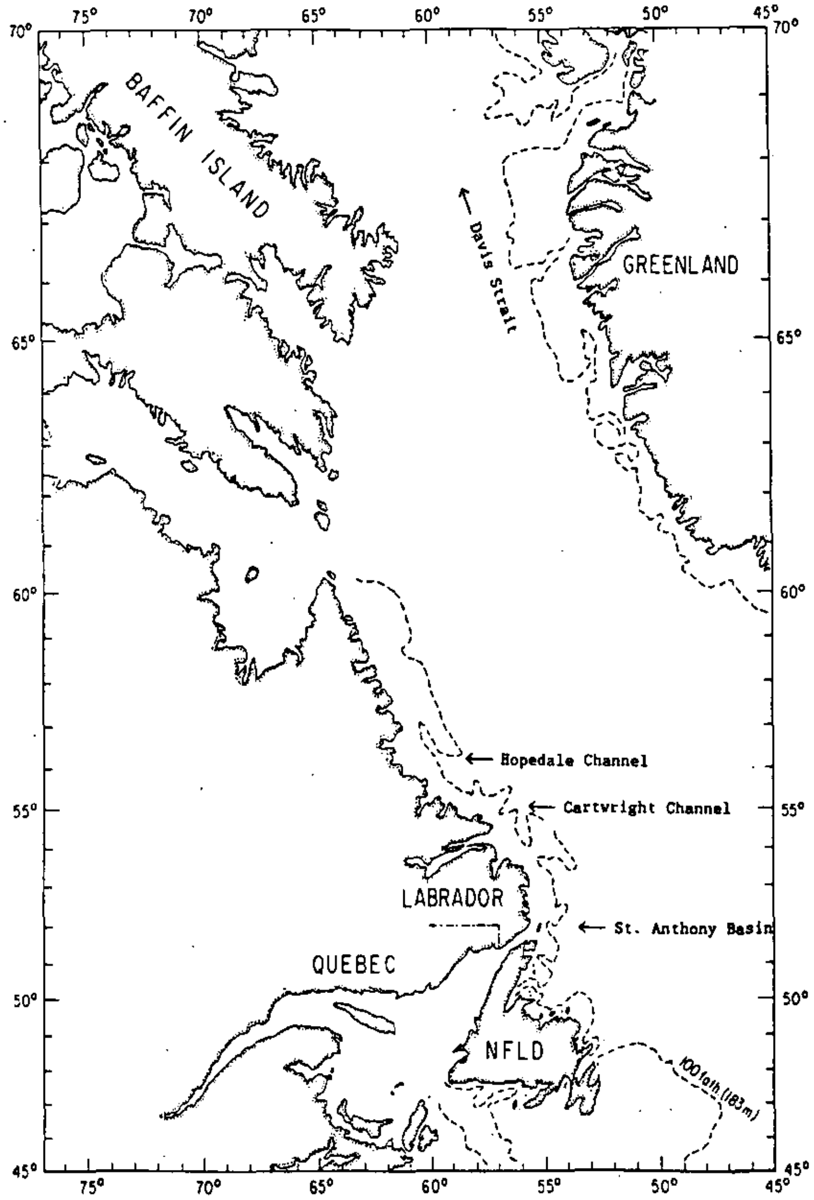


Fig.1. Areas in the northwest Atlantic from which samples of shrimp were compared for differences in growth.

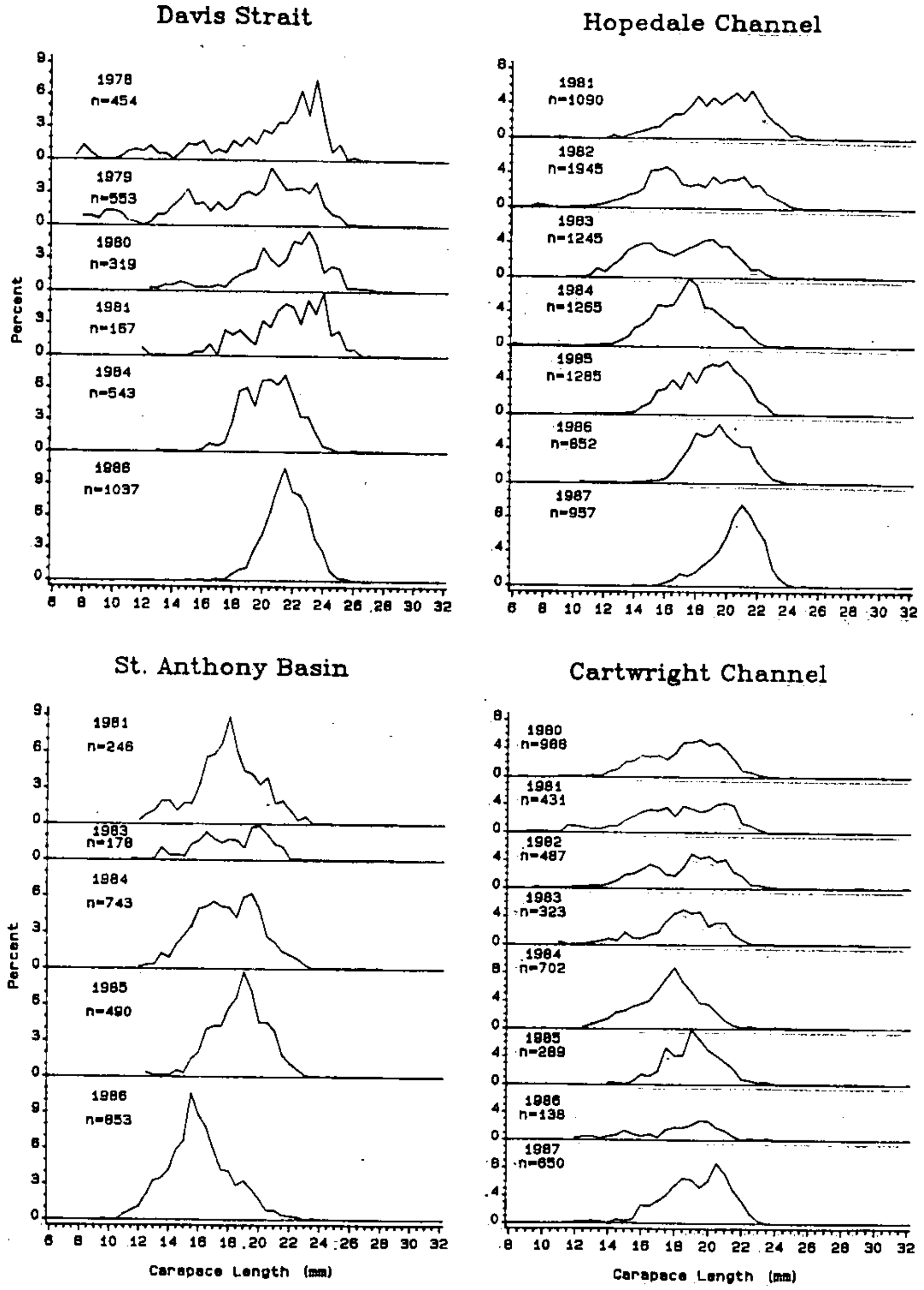
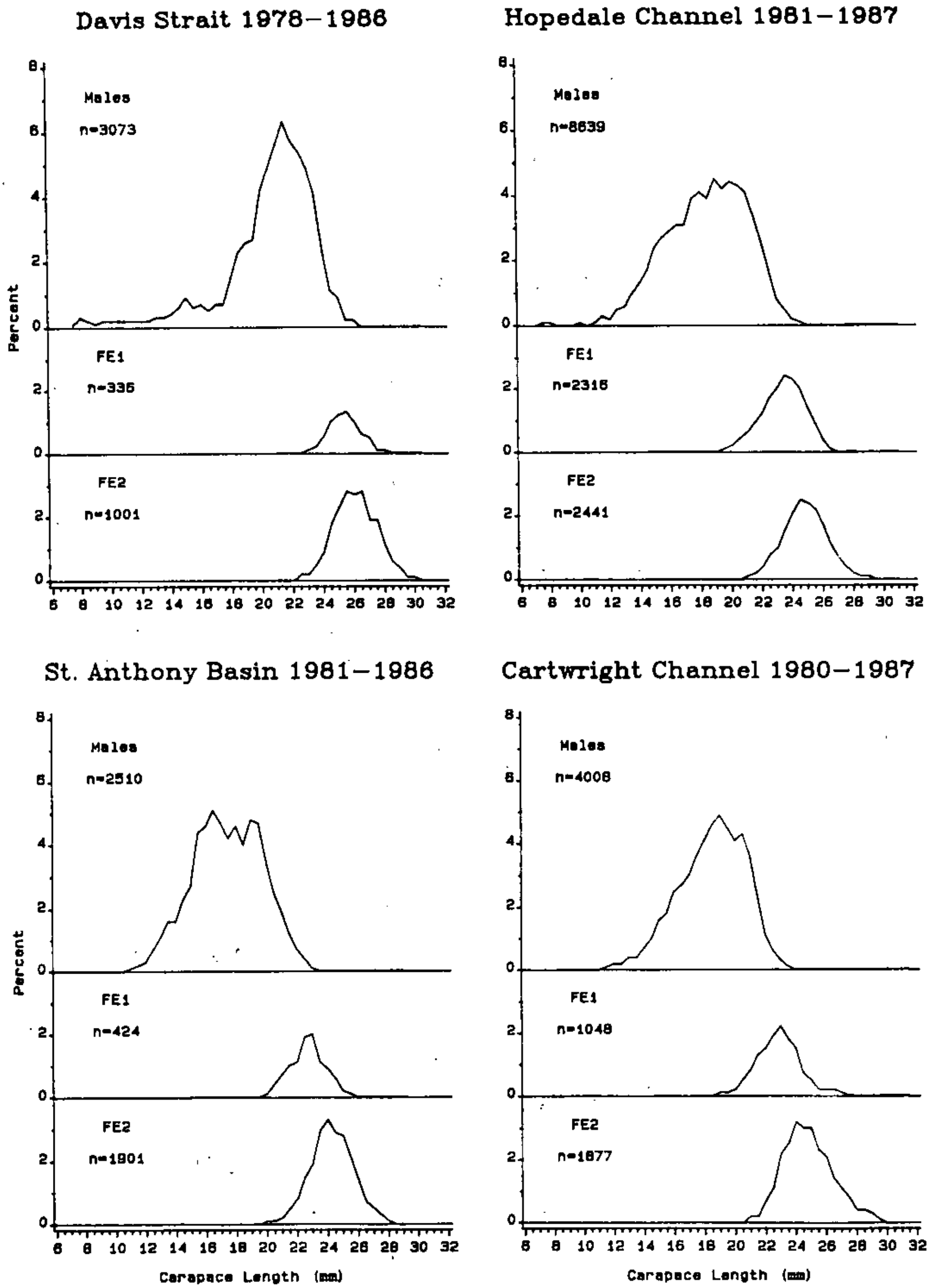


Fig.2. Length distributions of male shrimp from samples taken in four areas of the northwest Atlantic, 1978 - 1987.



Davis Strait 1978–1986

Hopedale Channel 1981–1987

St. Anthony Basin 1981–1986

Cartwright Channel 1980–1987

Fig.3. Pooled length distributions of male, primiparous (FE1) and multiparous (FE2) female shrimp taken in four areas of the northwest Atlantic.

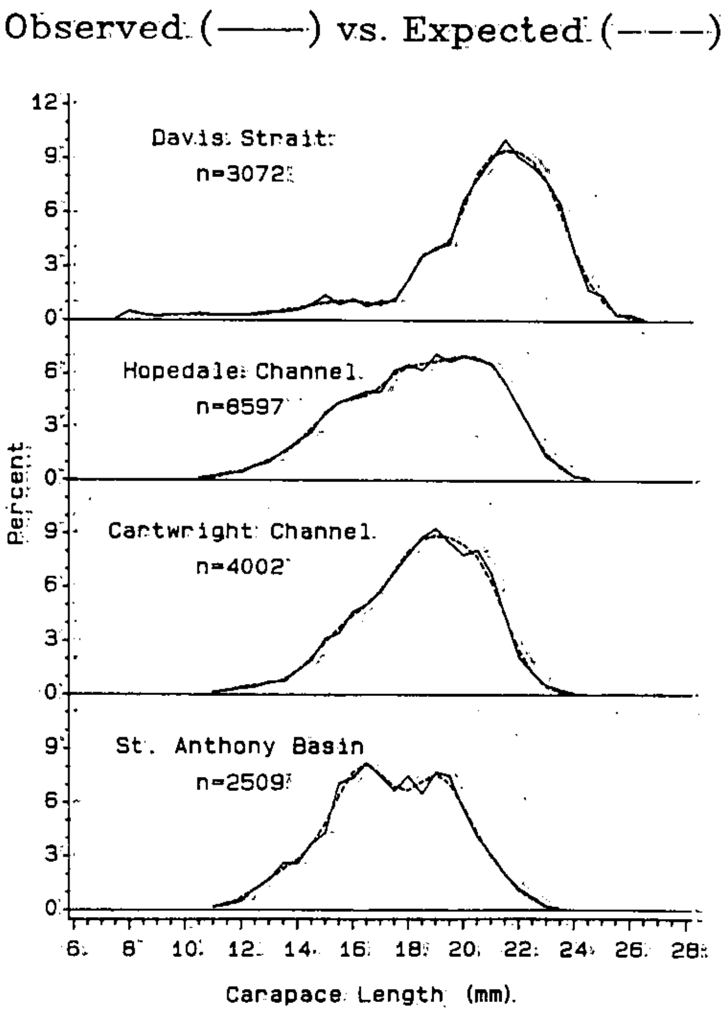


Fig. 4. Observed and expected length distributions of male shrimp from pooled samples taken in four areas of the northwest Atlantic, 1978 – 1987.