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The Female Sexual Maturity of Northern Shrimp (*Pandalus borealis* Kr.) in Denmark Strait in the Years 1985-1993 and a Comparison to the Nearest Icelandic Shrimp Populations.

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ABSTRACT

An account is given of the sexual maturity of *Pandalus borealis* in the years 1985-1993 as calculated from the logistic curve in the Denmark Strait as compared to the nearby offshore and inshore shrimp grounds. The L_{50}s of the Denmark Strait are by far the largest through all the years, or 27.9 mm on the average as compared to 23.8 - 24.3 mm for the nearest offshore Icelandic waters and 18.6 - 20.4 for the various inshore areas in the Icelandic waters.

INTRODUCTION

The Pandalids are generally protandric hermaphrodites, that reproduce first as males after which they change into females, and spawn as such for the rest of their life. In Icelandic waters all members of the species *Pandalus borealis* start as males and primary females have never been found there. Many authors have studied the maturity ogive of various species. Usually the ogive is calculated for separate sexes and the curve chosen is an s-shaped curve. Many investigators have used probit analysis to fit this type of curve (Bliss, 1934a). Also the method of Ashton (1972) has been popular, turning the proportions of mature females or males into so-called logits and fitting a straight line to those. As *P. borealis* changes sex Skúladóttir and Jónsson (1980) found it advisable to use the proportion of mature females (egg-bearing) against all as a basis for a maturity curve.

Rasmussen (1953) has indicated that the time at sex change is related to the size of individuals rather than the age but he considered that age at sex had considerable geographic variation. Appollonio *et al.* (1986) maintained that temperature plays a significant role in determining the time (age) of sex change. The findings of Skúladóttir *et al.* (1991) where the variation of female maturity in four areas within Icelandic waters were studied did support the last mentioned theory, but not quite the theory of Rasmussen that size at sex change is almost the same in different areas. Charnov and Anderson (1989) studied the size at sex change of northern shrimp in Pavlof Bay using the criterion proportion of females by length-classes, and maintained that there was great inter annual variation in both size at sex change and age due to variation in population size distribution. Skúladóttir *et al.* (1991) also studied the variation in size at sex change more accurately for all shrimp grounds in Icelandic waters in the years 1988 and 1989 using the sternal spines criterion and a straight line instead of the logistic curve to determine the length at which half of the shrimp had become mature females, termed L_{50}. The maturity line method was described by Skúladóttir (1990). Skúladóttir and Jónsson (1980) reported on L_{50} of P. borealis in various inshore and a few offshore areas in

Icelandic waters for the years 1977-1979, as well as on the variation within one fjord for the years 1961 -1980. The L_{50} was there calculated by using the proportion of egg bearing in each length-class, the S-shaped maturity ogive being drawn by eye.

In this study the L_{50}s of Northern shrimp in Denmark Strait are shown in the years 1985-1993, using the sternal spine criterion but fitting the logistic maturity curve directly to all samples within a month and area. For comparison there are results from the nearest Icelandic populations in the same years.

MATERIALS AND METHODS

Treatment of the biological samples

The samples of shrimp used here to estimate the maturity ogive were obtained both from commercial vessels and from surveys. More over about half of the Denmark Strait samples taken in September 1987 came from a Norwegian survey which was carried out by Odd Smedstad. A similar mesh size was used in all cases or 35 mm in the codend in the Norwegian survey and about 36 mm in the Icelandic sampling. The carapace of the shrimp was measured obliquely by sliding callipers, i.e. from the eyesocket to the hind edge of the carapace, middorsally (Rasmussen, 1953) to the nearest half mm. The samples where either measured fresh or first frozen and then measured.

Determination of the median maturity length

First the proportion of females without sternal spines (the definition of McCrary, 1971) against all specimens in a given length class is calculated and the same is done per every length class for each sample. In the autumn sexing in the strata 573 and 622 was based on the presence of egg bearing females (and a tiny proportion of green heads only in September). However this will not make any difference as all females in inshore areas spawn annually and are therefore after September all without sternal spines. Accurate sexing was also carried out based on the characteristic of the endopopod of the first pleopod (Rasmussen, 1953) although not necessary for this study. The method used to estimate the maturity ogive of mature females was based on fitting of the sigmoid, so-called logistic curve first described by Pearl and Reed (1920). The equation used is:

$$y = 1/(1+e^{-(a+bx)})$$

The logistic curve is fitted to all the samples within a month by using maximum likelihood iterations. From this the inflection point of the logistic curve was also calculated. It is the length where 50% (0.5) of the specimens are mature females. This carapace length is called median length or L_{50}. The mean L_{50} was then calculated for every area using the results of a month as one sample.

In order to see the difference in mean L_{50} between areas the variance of L_{50} values was calculated per area. The variances of every two areas compared were tested for differences using the methods described by Bailey (1959, pages 47-51). If the two variances were assessed to be equal judged by the variance ratio of the two areas, using the F-table (2.5%) the difference between the means was calculated in the traditional manner getting the value of t for the difference between the two means and comparing it to the appropriate t-value in the t-table. When the variance ratio of the two areas were assessed to be unequal by the F-table there was a more complicated method used to calculate the t-value for the difference.

RESULTS

The main strata numbers of the area investigated of both the Denmark Strait (str. nos. 626-628 and 676-678) and the Icelandic shrimp grounds are shown on Fig 1. On Fig. 2 the complicated system of ocean currents is shown. From the south comes the warm Irminger current and meet the cold East Greenland current in Denmark Strait goes west and mixes with the East Greenland current. This happens in south-eastern part of the tradtional area of the Denmark Strait shrimp. From the north comes also the East Icelandic current which is just as cold as the East Greenland current and is prominent just north of Iceland. The coastal current of Iceland is warmest at the south coast but gets gradually colder when proceeding further clockwise around the country and thus meeting the cold east Icelandic current.

One maturity ogive has been fitted to all available samples in the same month and area. Thus there are as many points (representing proportions of mature females) per length-class as there are samples. Most of the maturity ogives that have been fitted for this paper are shown on Figs. 3-7 in the years 1985 through 1993. Maturity ogives of Denmark Strait are presented in these figures. Also shown on Figures 3-7 are the maturity ogives from the offshore area Nordurkantur (strata nos. 720-724). Scattered in between on Figures 5, 6 and 7 are maturity ogives from other areas, like the offshore area Hali (strata nos. 674 and 675) first fished in 1990. This area is the nearest of the Icelandic offshore areas to that of the Denmark Strait. On Figs. 6 and 7 the nearest inshore areas Isafjardardjup (stratum no. 622), Arnarfjordur (str. no. 573), Snaefellsnes (str. nos. 474-475 and 523-524) and finally Eldey (str. no. 373) are shown. In Table 1, the L_{50}s of the shrimp in the Denmark Strait area are listed as well as the L_{50}s of other previously mentioned areas. Thus the L_{50}s of shrimp in the Denmark Strait can be compared to those of Nordurkantur when samples are available in the same months. The L_{50}s of Nordurkantur are generally 3.5-4.6 mm smaller than those of Denmark Strait except in May 1992 where there is a difference of only 2.2 mm. In spite of there being a short distance between the Denmark Strait area and Hali (strata nos. 674 and 675), there is a deep trough between, there is a similar difference in L_{50}s between those as between the Denmark Strait and Nordurkantur. Alas there are no samples from both the Denmark Strait and Hali in the same months except for July 1990 (Fig. 4), but there are samples from Hali and Nordurkantur either in the same months or adjacent months showing very similar results.

The L_{50}s of the inshore areas are again much smaller than those of the last two last mentioned areas offshore, namely 17.6-19.8 mm for Isafjardardjup (stratum no. 622), 18.2-21.8 mm for Arnarfjordur (stratum no. 573), 17.2-22.1 for Snaefellsnes (strata nos. 474, 523-524) and 18.8-22.3 mm for Eldey (stratum no. 373). The number of specimens studied in every month used in this paper is listed in Table 2.

In Table 3 there are presented the two way variance analysis of all areas. There was a significant difference between the mean L_{50} of Denmark Strait as compared to that of every other area. The mean L_{50} of Nordurkantur (str. nos. 720-724) was also significantly different from all other areas. The mean L_{50}s of all inshore areas were not significantly different from each other except for those of Isafjardardjup and Eldey.

DISCUSSION

The female maturity of Northern shrimp has been studied before in the Icelandic waters. Although Jónsson and Hallgrímsson (1981) did not use the sternal spine criterion they found that the L_{50} of the Denmark Strait shrimp was between 28 and 28.5 mm for August-October in 1979 and 1980 combined, but again in Denmark Strait 20-30% of the mature shrimp do not spawn annually so their approximated L_{50}s were slightly overestimated.

In later studies the L_{50} has been calculated first per each sample and then the average L_{50} per area and month have been calculated for the years 1988 and 1989 (Skuladottir et al, 1991). Instead of a maturity ogive a maturity line (straight line) was used but the results of L_{50} were similar. Looking at all the L_{50} data there seem to be some stability in most areas as regards the L_{50} in the temporal sense.

Seasonallity in the L_{50} size of shrimp in the Denmark Strait would be expected, namely a small decrease in L_{50} when a new batch of females looses the spines and joins the group of females about to spawn in July-August (Jónsson and Hallgrimsson, 1981, but there are no definite indications of it in this paper. On the whole the L_{50} has not changed in the Denmark Strait through the years to any great extent. The only exception is in September 1990 where the L_{50} is 26.5 mm. The mean L_{50} of shrimp in the Denmark Strait per annum was highest in 1989 and lowest in 1990 (Skúladóttir 1993). It can be speculated what caused this. There could have been an influx of shrimps in September 1990 from strata numbers 720-724 or 674-675 to the Denmark Strait area, bringing smaller mature females than are usually seen there. Another possibility is an early sex change. Rasmussen (1953, 1969) observed two modes of transitionals in the same population indicating that not the whole year-class would change sex in the same year. Horsted and Smidt (1956) also noted something similar. The former theory seems more plausible as the L_{50}s for the Denmark Strait were quite normal both in July 1990 and May 1991 which is within the same breeding season, namely 27.6 and 28.5 mm respectively.

In the Icelandic waters temperature and L_{50} appear to be roughly inversely related (Skúladóttir *et al.* 1991). Thus the L_{50} at strata 720-724 is 23.0-24.9 mm where the average near bottom temperature for the period 1974-1989 was 0°C. In Isafjardardjup (str. no. 622) the mean near bottom temperature was 4.5 °C and L_{50} is between 17.6-19.8 mm. Snæfellsnes (str. nos. 47,523-524) had the near bottom temperature of 6 ° in the 1991 study as the warm Irminger current is very prominent there and the L_{50} is between 17.2 and 22.1 mm. The shrimp grounds in the Denmark Strait seem to coincide mainly with the area which is covered with the so-called Arctic intermediate layer (Gade et al 1965, Stein 1984) the temperature being between 0 and 2°C. Thus the very large L_{50} does not seem to occur at the lowest temperature found.

The first attempt to determine the age of the Denmark Strait shrimp has been carried out using the Elefan program (Smedstad 1990). According to Smedstad the females are 6 years old when they spawn for the first time. Skuladottir (1994) has carried out some preliminary age determination of the Denmark Strait shrimp and considers the possibility of females being generally one year older than assessed by Smedstad or 7 when they spawn for the first time. This could then be one year older than those of the Nordurkantur shrimp which spawns for the first time at the age of 6 according to the preliminary ageing (Skuladottir *et al.*, 1991). For comparison the shrimp in both Snaefellsnes (Skúladóttir et al 1991) and in Isafjardardjúp is generally considered to spawn at the age of 3 for the first time.

The L_{50} and size at first spawning is not the same by definition as the size at first spawning. The latter is usually slightly larger than the L_{50} for the same sample. As authors have not published any L_{50} values on *P. borealis*, the comparison has to be to the size at first spawning. The age and approximate size of females spawning for the first time at Nordurkantur is thus not very far from some of the areas in the Northwest Atlantic, like St. Antony Basin where females are thought to spawn at the age of 6 and the mean length of the multiparous females is 24.1 mm for the years 1981 and 1983-1986 (Parsons *et. al.*, 1989). There the average annual bottom temperature ranges from 2° to 4°C (Parsons *et. al.*, 1989). The mean size of multiparous females is 26.2 mm for the Davis Strait shrimp, the age being 7 or 8 years at first spawning (Parsons et. al., 1989), where the bottom temperature ranges from 1° to 4°C. The Denmark Strait shrimp is as far as known the largest of all *P. borealis* in the world when it changes sex, namely with the L_{50}, 27.9 mm on the average. The Northern Shrimp of the Bering Sea is almost as large, namely 27 mm (age 5.5) when spawning for the first time as a female (Ivanov 1969), and the average annual temperature is there about 1.7°C. The Barents sea is considered by Teigsmark (1983) to have three populations growing with a different rate and spawning for the first time at the ages 4.5, 5.5, and 6.5 years respectively. The temperature is 3°, 2°, and 1°C approximately in each area. The size at first female maturity is not very variable there between the populations, namely from 20.5-21.4 in the years 1978 and 1979 (Teigsmark, 1983) largest in the coldest area. (The inshore shrimp in Icelandic waters e.g. in Isafjardardjup and at Snaefellsnes, where bottom temperature is 4.5 and 6°C respectively, the shrimp spawns for the first time at the age of 3.5 years and the L_{50}s are 17.7-20.1 mm). In the North Sea the females spawn at the age of 1.5 years where the average annual temperature is about 6°C and the size at first spawning is 17.0 to 17.8 mm (Anon. 1988).

The findings in this paper agree to some extent with the generally accepted theory, as other authors have also found, namely increasing longevity and slower growth with higher latitudes and decreasing temperatures (Rasmussen 1953, Appolonio and Dunton, 1986). However the difference in growth rate does not result in sex change occurring at a similar size in different areas, as Rasmussen considered (1953). Charnov (1982) has shown that with increasing latitude the length of time spent as male increased.

CONCLUSION

There seem to be at least 3 regimes of environment covered by this paper, giving constantly rise to three size categories of L_{50} namely the Denmark Strait which has the range of L_{50} between 26.5 mm and 29.3 mm where bottom temperature might be 0-2°C. The offshore strata 720-724 with the average bottom temperature of 0°C where the median maturity length is between 23 and 24.9 mm. and the inshore and areas where temperature ranges from 4.5-6 °C at the west coast where L_{50} is always below 22 mm and usually between 17.0 and 21.4 mm, and the first female spawning is generally at the age of 3 years with the exception of the cold threshold fjord Arnarfjordur. The consistency in L_{50} is such that the mean L_{50} can be used as a criterion of a stock.

There appears to be an inverse relationship between temperature and size at first spawning or L_{50} in the very few areas in Icelandic waters where average bottom temperature has been calculated for a long series of years.

So not only is there a geographic variation in growth and longevity of northern shrimp, but also there is a some variation in the size at first spawning of females.

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Table 1. The L_{50} (mm) of northern shrimp by month and year in the Denmark Strait as compared to the L_{50} of the most ajacent areas in the Icelandic waters.

	STRATA						
Year Month	627-629 676-679	674-675	720-724	622	573	474 523-524	373
1985							
July	28.3					20.0	20.7
August	27.5		23.4				21.1
Sept./Oct.				19.8	20.5	21.3	21.6
November	27.3			19.6	21.8		
December	27.7						
1986							
September			23.7			20.5	20.8
October	27.3			18.7	18.8	21.7	20.8
December	28.8			19.1	18.2		
1987							
September	27.6		23.0			21.2	21.7
October	29.3			19.0	19.4		22.3
November	28.3			19.8	21.5		
December	28.6			19.4	18.9		
1988							
August	28.3		23.9			19.9	21.4
September	27.9		24.0		19.4		
October				19.3			
1989							
May	28.8					17.2	
June			24.8				18.8
1990							
July	27.6	24.4	24.1			20.4	20.1
September	26.5				19.1	22.1	21.5
October				17.6			
1991							
April				18.6		18.9	
May	28.5						19.6
1992							
Mars			24.4		19.6		
April	27.7			19.2			
May	27.1		24.9			18.3	19.5
July		24.0	24.0				
October				18.2	19.9	20.1	21.4
November			23.5	18.6		19.8	
December		24.5		18.3			
1993							
Mars				18.5			
April	27.4		24.1	19.4		18.8	
May	27.1		23.4			17.7	20.3
Mean	27.9	24.3	23.9	18.9	19.7	19.9	20.8
Number	20	3	13	16	11	15	15
Standard error	0.16	0.15	0.15	0.16	0.34	0.37	0.25

Table 2. The number of shrimp used for the calculation of L_{50} in the same strata and months as shown in table 2.

Year Month	STRATA						
	627-629 676-679	674-675	720-724	622	573	474 523-524	373
1985							
July	402					1621	1454
August	395		407				1038
Sept./Oct.				4679	608	1913	1805
November	941			3024	2306		
December	138						
1986							
September			3142			312	788
October	210			4701	1515	224	360
December	123			1029	1020		
1987							
September	2357		670			302	658
October	151			6712	2902		908
November	2759			4870	404		
December	260			1016	1498		
1988							
August	177		3355			568	1194
September	485		1019		2241		
October				10599			
1989							
May	116					1579	
June			7497				302
1990							
July	810	979	7624			1180	210
September	1779				4583	453	588
October				13069			
1991							
April				2082		3347	
May	1719						2088
1992							
Mars			827		196		
April	696			1105			
May	455		1944			3183	2042
July		950	9180				
October				14063	5457	573	241
November			1372	2726		272	
December		553		320			
1993							
Mars				1516			
April	1286		451	760		2580	
May	105		551			1993	2556
Mean	768	827	2926	4517	2066	1340	1082

Table 3. The comparison of mean L_{50} of two areas at a time. The calculated t-value is denoted t. Significant difference is denoted signif. and number of degrees of freedom is denoted f.

Strata numbers	720-724	622	573	474 523-524	373
627-629 676-679	t=17 f=31 signif.	t=39.7 f=34 signif.	t=27.3 f=33 signif.	t=17.5 f=19 signif.	t=25.2 f=33 signif.
720-724		t=22.6 f=28 signif.	t=11.3 f=14 signif.	t=10.1 f=19 signif.	t=10.48 f=26 signif.
622	t=22.6 f=28 signif.		t=2.5 f=14 not signif.	t=2.3 f=19 not signif.	t=6.4 f=29 signif.
474 523-524	t=10.1 f=19 signif.	t=2.3 f=19 not signif.	no difference		t=2.0 f=28 not signif.
373	t=10.48 f=26 signif.	t=6.4 f=29 signif.	t=2.5 f=24 not signif.	t=2.0 f=28 not signif.	

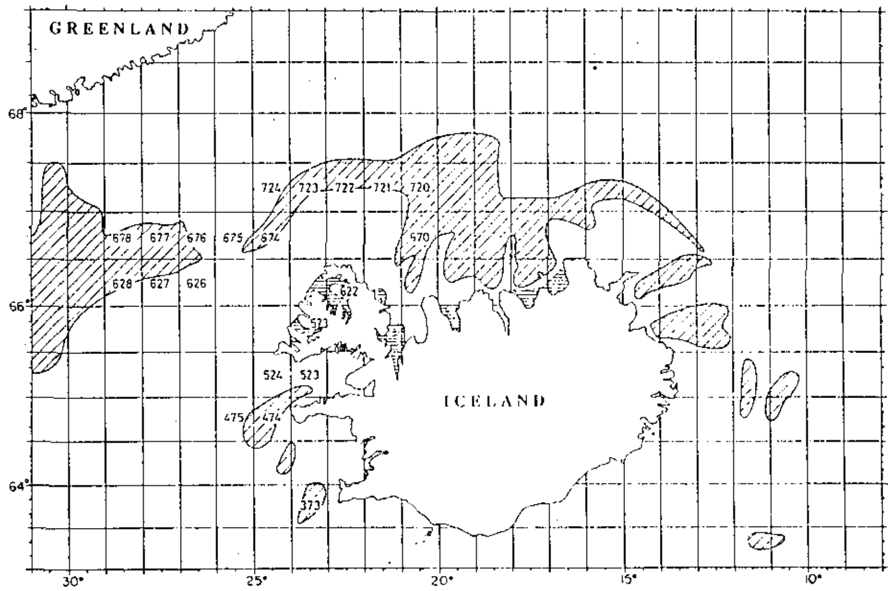

Figure 1. The shrimp grounds in Denmark Strait and Icelandic waters. Strata numbers used in the paper are shown on this map.

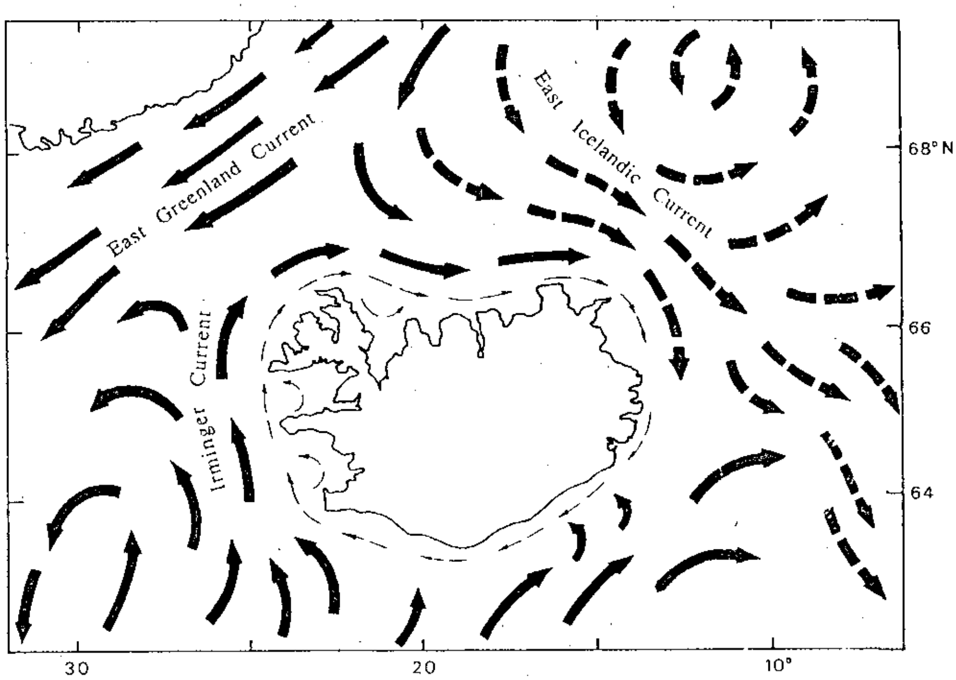

Figure 2. The three main ocean currents around Iceland. The two currents coming from north are cold and the current coming from south is warm. The coastal current is indcated by fine arrows. The figure is adapted from Gunnarsson (1991).

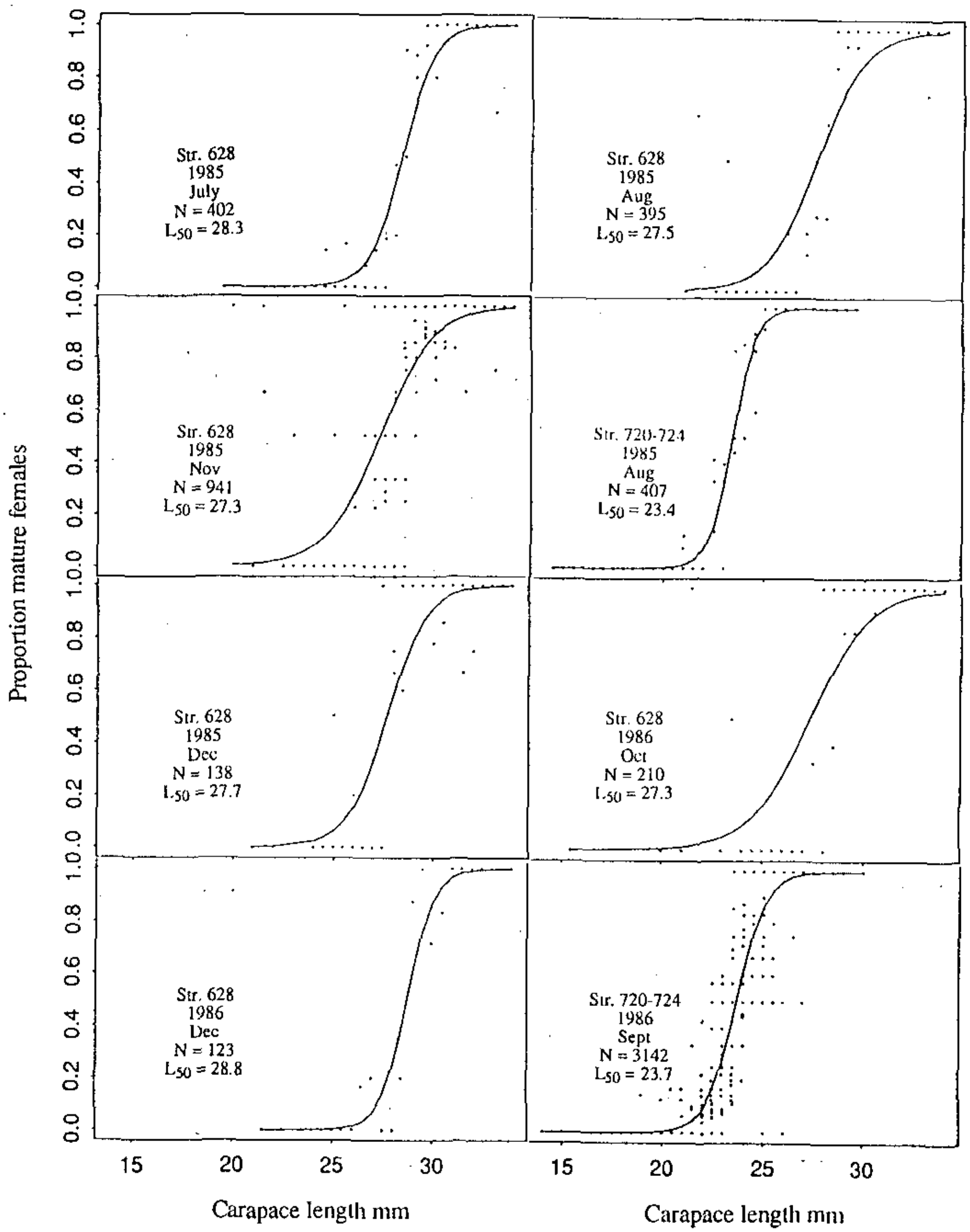

Figure 3. The female maturity ogives in Denmark Strait (strata no. 628) and Nordurkantur (strata nos. 720-724) in 1985 and 1986 by months.

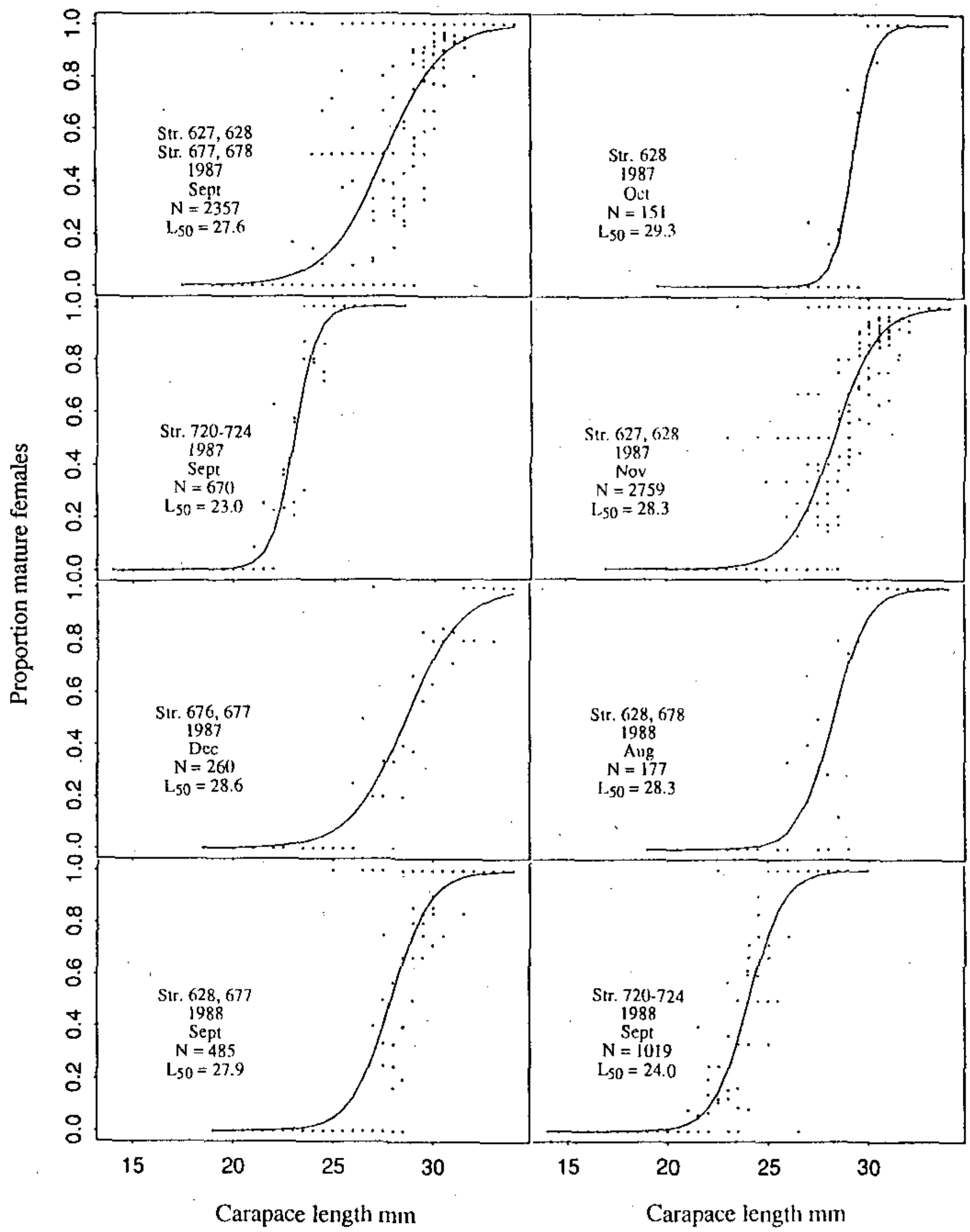

Figure 4. The female maturity ogives in Denmark Strait (strata nos. 627, 628, 677 and 678) and Nordurkantur in 1987 and 1988.

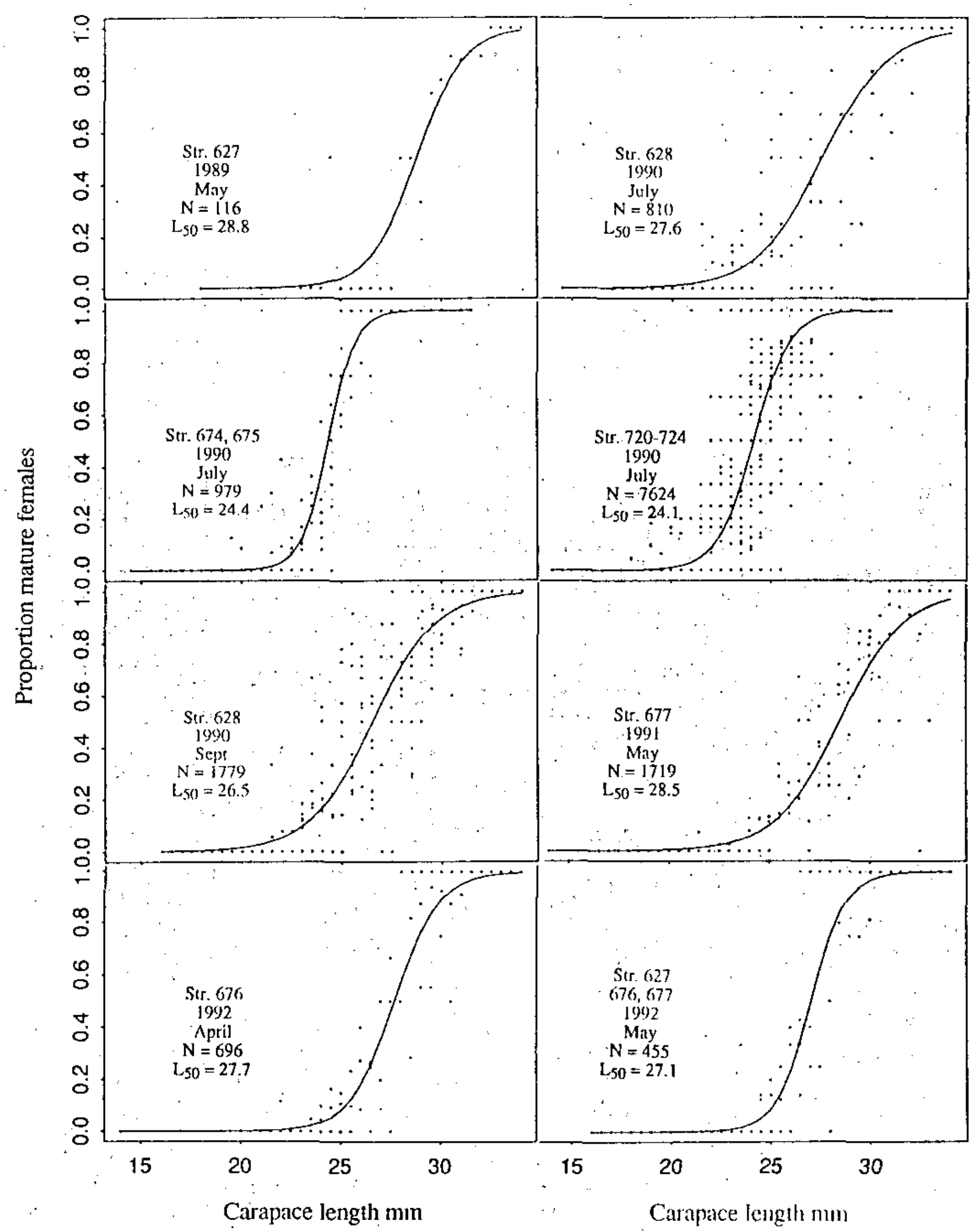

Figure 5. The female maturity ogives in Denmark Strait and Nordurkantur in the years 1989-1992.

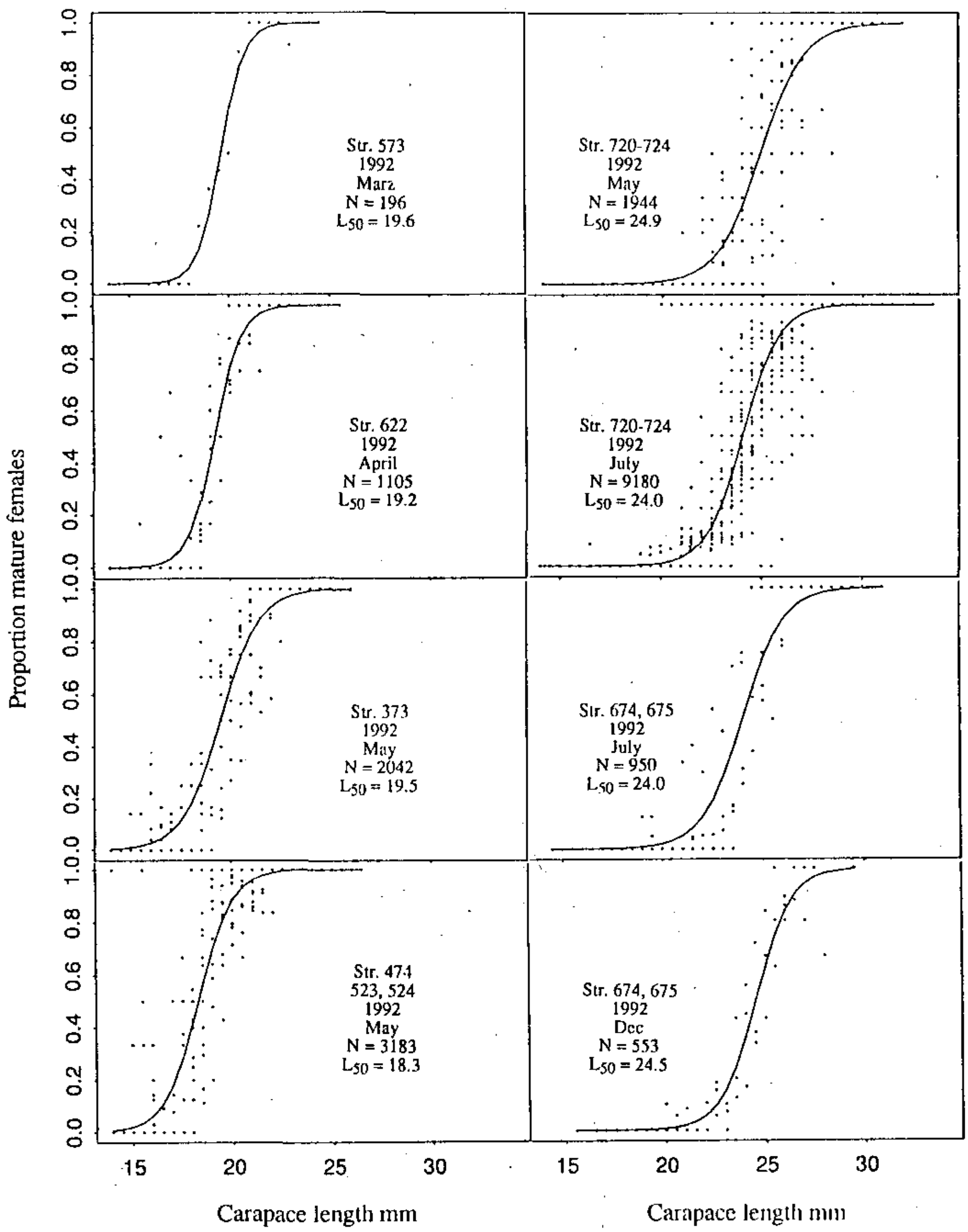

Figure 6. The female maturity ogives in various inshore west coast areas and the offshore areas Hali (strata nos. 674 and 675) and Nordurkantur in 1992.

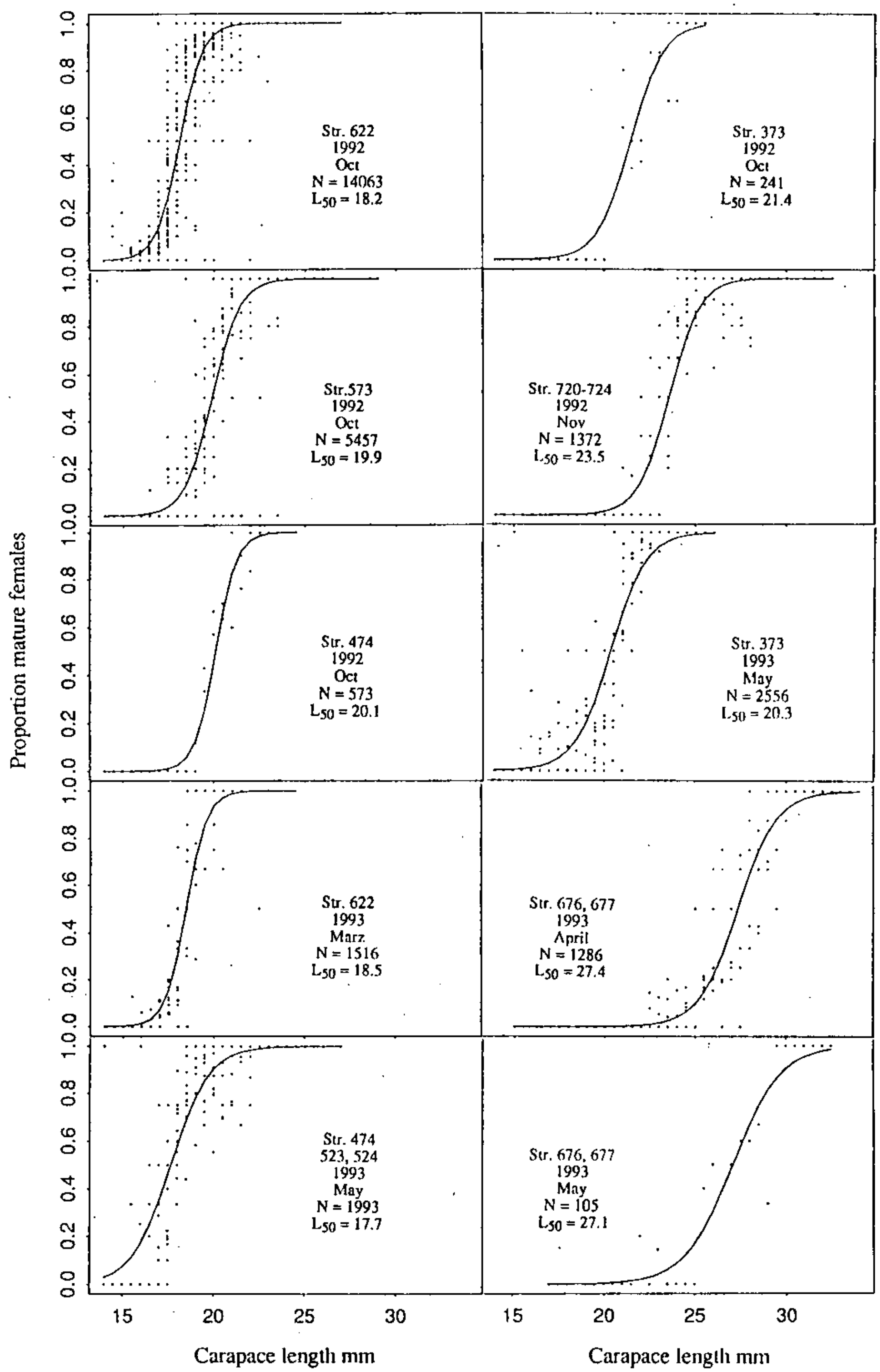

Figure 7. The female maturity ogives in various inshore west coast areas, the offshore area Nordurkantur and Denmark Strait in 1992 and 1993.