

**THE VARIATION IN SIZE AND AGE AT CHANGE OF SEX, MAXIMUM  
LENGTH AND LENGTH OF OVIGEROUS PERIODS OF THE SHRIMP,  
*PANDALUS BOREALIS*, AT DIFFERENT TEMPERATURES IN  
ICELANDIC WATERS.**

By

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**ABSTRACT**

The carapace length where 50% of *Pandalus borealis* are mature females, termed L50 was calculated from a simple line fitted to the measured data of each sample for the years 1988 and 1989. Average L50s for unit areas off North Iceland indicate a general trend towards increased L50 going from shallow to deeper waters, the highest L50 occurring in the deep cold water furthest north in the areas Nordurkantur and Kolbeinsey.

This trend was consistent both the two years investigated. To a certain extent there seems to be a relationship between the near-bottom temperature and the L50 of *P. borealis*. Average L50 for *P. borealis* in the warm inshore areas was found to be much lower than in the colder offshore areas. By comparing the average L50, the associated 95% confidence limits and geographical position, the twelve offshore areas could be combined into five super-areas. Similarities and/or differences in L50 among inshore areas were not consistent during the two years investigated. Thus the criterion of L50 was not found to be useful for distinguishing between the inshore populations.

An average annual near-bottom temperature, for the years 1974-1989, has been calculated for four areas. The length of the ovigerous period, also a mean of many years, and the age (length) at first spawning as females, was found to be related to temperature. Thus the ovigerous period ranged from 5.5 months at the mean annual temperature of 5.98 C west of Iceland to 10 months at the mean annual temperature of -0.01 C in the northern-most area. The range of age at first spawning was estimated to be from three to six years, with a small proportion spawning at the age of two in one area.

**INTRODUCTION**

The Pandalids are generally protandrous hermaphrodites, that reproduce first as males but later change to females, and spawn as such for the rest of their life. Rasmussen (1953) and Fox (1972) have indicated that the time at sex change is related to the size of individuals rather than age. Rasmussen (1953) also considers temperature to play a significant role in the rate of growth of *Pandalus borealis*. Thus the age at first spawning could vary a great deal. Skúladóttir and Jónsson (1980) reported on L50 in various inshore and few offshore areas in Icelandic waters for the years 1977-1979, as well as on the variation within one area for the years 1961-1980. Skúladóttir (1990) has shown that the size at which 50 % of males have changed sex to mature females varies significantly between areas and appears to be influenced by temperature in the surroundings. The age at first spawning of females was first assessed by Sigurdsson and Hallgrímsson (1965) in Icelandic waters in Ísafjardardjúp. Allen (1959) was the first to compare the length of ovigerous periods of *P. borealis* in widely different latitudes and put these into context with temperature. In Icelandic waters Sigurdsson and Hallgrímsson (1965) estimated the length of the ovigerous period in Ísafjardardjúp and Skúladóttir *et al.* (1978) reported on the length of the eggbearing period in various inshore areas in Icelandic waters.

In this study a more detailed examination of various biological factors of *P. borealis* in Icelandic waters was made. Factors, such as size at sex change, age at first spawning and length of ovigerous periods were particularly investigated along with the possible relationship between these biological factors and environmental temperature.

## MATERIAL AND METHODS

### THE HANDLING OF SAMPLES

The collections of shrimp used here for the calculation of the maturity line (see below) were obtained mostly during annual surveys of the shrimp grounds in the years 1988 and 1989, either just prior to spawning or shortly after. Areas 1 and 8 are exceptions from this as no samples were available in October or November in the years 1988 and 1989 (Table 1). All specimens were measured to the nearest half mm carapace length (CL) and then graded into nine sexual categories, males, transitionals, and seven stages of females. The female stages were divided into two major categories, with or without sternal spines (MacCrary 1971). The females with sternal spines were then divided into two categories, with headroes (termed maturing females) and without headroes. The females without sternal spines, hereafter also called mature females, were graded into 5 categories, i.e. females with headroes, females with external eggs but no eyes visible in the eggs, females with eyes visible in the eggs, females having headroes as well as external eggs (eyes visible) and females just without spines. Exception from this grading into nine categories were inshore samples taken during September through December. Our previous experience of many years has shown that in inshore areas during this time of the year almost all female *P. borealis* are either egg-bearing or having headroes and all other shrimps are males with few exceptions. This allowed the inshore samples from September through December to be graded into three categories: females with headroes, females with external eggs and what was left was considered males.

### THE CALCULATION OF L<sub>50</sub> AND max L

The proportion of *P. borealis* without sternal spines to all specimens in the same length class was calculated. These proportions were plotted against carapace length, and a simple straight line was fitted to each sample (Skúladóttir 1990). When fitting the line, only the part of the length distribution, including mature females was used. The lower limit was chosen two length classes before the presence of mature females and similarly the higher limit two length classes after all specimens had become mature females. When the length distribution was discontinuous at the top, with two or more length classes containing no specimens, the occasional shrimps occurring in higher length classes were omitted. The occasional parasitized females without sternal spines were also omitted if they occurred below the part of the length distribution containing mature females. After estimating the L<sub>50</sub> for each sample the average L<sub>50</sub>, the standard error (SE) and confidence limits were calculated for all areas. Only the estimates of L<sub>50</sub>, where the fit of the maturity line was significant at the 0.05 level of probability were used. Therefore the number of samples stated in table 3 for L<sub>50</sub> can be lower than that of same areas for max L in table 4. The average max L of an area was calculated from the max L of each sample. Also the standard error and confidence limits were calculated for all areas.

### OVIGEROUS PERIODS

In offshore areas 10 and 15, data on seven ovigerous periods were collected in 1983 to 1990. The long ovigerous period in the offshore areas complicates the pattern of development. In June and July for example, both females with eyed external eggs and newly spawned eggs were present. Because of this the proportion of egg-bearing females was calculated in a different way depending on the stage of the ovigerous period:

1. Proportion of females with external eggs, no eyes, to all females and transitionals for the period May through June.
2. Proportion of females with external eggs, no eyes, to all mature females and females with headroes also having sternal spines for the period July through September.
3. Proportion of females with external eggs to all mature females for the period October through March next year.
4. Proportion of females with external eyed eggs, to all mature females for the period April through July.

In area 4 and 8 data were collected for 8 ovigerous periods, from 1982 to 1990, and in area 8 for 3 additional ovigerous periods during 1973-1980. To estimate the onset of spawning in the inshore areas the proportion of egg-bearing females to that of all females either with headroes or egg-bearing was calculated. The hatching in areas 4 and 8 was calculated from the proportion of females with external eggs to all mature females. For two months at the beginning and the end of each ovigerous period the average proportion of egg-bearing females was calculated on a monthly basis. Finally an average proportion of egg-bearing females was calculated for each week or month in each area. Length of the ovigerous period was estimated from the time when half of the maturing and mature females had spawned, until half of the mature females had liberated their larvae. As a complete set of data for each of the ovigerous period was not available, a composite average was calculated on a weekly or monthly basis using available data for that particular week or month for the period of years in question.

## TEMPERATURE

In order to examine a possible relationship between temperature and the ovigerous period as well as L50 of *P. borealis*, information on near-bottom temperature of four chosen areas (No. 4, 8, 10 and 15) were extracted from the temperature data base collected by the Marine Research Institute of Iceland in the years 1974-1989. The temperature at various depths at the available hydrographic stations that corresponded to the range of depth of shrimp grounds in these four areas were used. For each area the average temperature of different depth strata was first calculated for each month of the years 1974-1989. From these averages the average monthly temperature for these years was calculated. Average annual near-bottom temperature of each area was derived from these average monthly temperatures.

## AGE DETERMINATION

All length measurements of *P. borealis* collected in areas 10 and 15 during annual shrimp surveys in 1988 and 1989 were combined for each year and area. Measurements of samples from area 4 were combined by months throughout the winter of each year (Skúladóttir *et al.* 1989). The length distribution of shrimp was always divided into at least two categories, i.e. mature females and the rest. In case of the offshore shrimp the rest was further graded into the categories males on one hand and transitionals and immature females on the other. By doing this, the age-determination was made more easy. The age determination was carried out by the method of MacDonald and Pitcher (1979).

## RESULTS

The proportion of mature females was variable between areas in 1988 and 1989. In 1988 it ranged from 6.5% in the offshore area 17 to 45.5% in inshore area 3, but in 1989 it ranged from 9.2% in the offshore area 16 to 36.2% in inshore area 3 (Tables 1 and 2). In the Denmark Strait in 1988 the proportion of females was higher than in any other area, 73.6%. Generally, higher proportions of mature females were found in inshore areas as compared to offshore areas. Extensive variations in these proportions were observed between years within some of the areas. The general trend was towards increased proportions of females in inshore areas, but decreased proportions in offshore areas. The greatest changes in inshore areas were found in area 1 where the proportion increased from 7.7% in 1988 to 26.1% in 1989, and in area 7 where it increased from 11.9% in 1988 to 29.4% in 1989. In offshore areas the greatest changes were found in area 12 where the proportion decreased from 23.2% in 1988 to 14.5% in 1989 and in area 14 where it decreased from 31.2% in 1988 to 12.9% in 1989.

The L50 for *P. borealis* was found to be lowest in the fjords at the northwest and north coasts (areas 3-7) ranging in 1988 from 17.02 to 19.24 mm and in 1989 from 16.40 to 19.84 (Table 3, Figs. 2 and 3). In three of these areas (areas 3, 5 and 6) the changes in L50 from 1988 to 1989 were relatively small, but in area 4 it dropped from 19.13 to 16.40 mm and in area 7 it increased from 18.08 to 19.64 mm. The values for L50 in areas 1 and 8 at the west coast were similar, 20.71 and 19.63 mm respectively in 1988 and 19.54 and 20.01 mm in 1989. These values are close to the largest L50 found in the inshore areas at the northwest and north coasts (Figs. 6 and 7). In the offshore area off North and East Iceland the lowest value for L50 was found in the unit area closest to the shore in area 15, 21.0 mm in 1988 and 20.1 mm in 1989 (Figs. 2 and 3), but only one sample was available in this unit area each year. In 1988 the

highest value for L50 in a unit area was found in area 13 (24.4 mm), but in 1989 in area 10 (25.3 mm). The average L50 for unit areas off North Iceland indicate a general trend towards increased L50 going from shallow areas to deeper waters. This trend was consistent for both years and is well demonstrated in the western part of the offshore area, areas 11 and 10, where L50 increased from 22.1 to 24.0 mm in 1988, and from 21.7 to 24.9 mm in 1989, going from the southern-most unit area of area 11 to the deeper waters further north in area 10 (Figs. 1, 2 and 3). The increase in L50 becomes even more conspicuous if inshore area 5 is included in this comparison, since the L50 values were only 17.69 and 17.55 in this area in 1988 and 1989 respectively. However in nearshore areas with deep trenches the value for L50 was relatively high as in area 14. In spite of a gradient like increase in L50 from shallow to deep waters, the unit areas could be combined to form larger areas, areas 10-20, based on similarities in L50 and geographical positions (Table 3, Figs. 1, 6 and 7). Comparing L50 of *P. borealis* in these areas and in the fjords of the northwest and north coasts it becomes clear that L50 is distinctly higher in the offshore areas than in the fjords (areas 3-7). By further grouping together geographically continent areas with similarities in mean L50 of *P. borealis*, the offshore areas can be grouped into five super areas:

1. Areas 10 and 13 with L50 values of 24.92 and 24.81 mm respectively in 1989.
2. Areas 11 and 12 with L50 values of 23.58 and 23.45 mm respectively in 1989.
3. Areas 15 to 19 with L50 values ranging from 22.31 to 22.63 mm in 1989.
4. Area 20 with L50 value of 23.80 mm in 1989 which is similar to that of super area 2, but is geographically distinct from that area.
5. Area 9 with L50 value of 28.09 mm in 1988, but no data for that area were available for 1989. This was the highest mean L50 found in Icelandic waters in 1988.

Off the northern coast, where the first three super areas come together, there is area 14 with L50 value of 24.20 mm in 1989. This is close to the values found in super area 1, and area 14 should perhaps be included there. In the offshore areas L50 values have increased from 1988 to 1989. This is consistent for all areas ranging from 0.39 to 1.25 mm and not affecting the similarities or differences between areas when viewed for each year separately.

The average maximum carapace length (max L) of *P. borealis* in unit areas of the offshore area did not show a pattern of increased value going from near the coast to the deeper waters further offshore as was the case with L50 (Figs. 4 and 5). However after combining unit areas into larger areas a slight trend towards average max L being largest in areas furthest offshore, namely areas 10, 13, 14 and 20, was observed. A small increase from 1988 to 1989 in average max L was found in all offshore areas, except area 18. Average max L of *P. borealis* in the fjords at the northwest and north coasts, areas 3-7 and at the west coast (areas 1 and 8) was distinctly lower than in the offshore areas (Table 4).

The ovigerous period of *P. borealis* was found to differ between the four areas investigated (Fig. 8). This difference in ovigerous period seems to be related to difference in average temperature between the areas (Table 5). Area 8 had the highest mean annual near-bottom temperature, 5.98 C, and the shortest ovigerous period of about 5.5 months. Area 10 had the lowest temperature, -0.01 C, and the longest egg-bearing time, 10 months. There seems to be a considerable variation in the relationship between egg-bearing time and average near-bottom temperature. The difference in temperature between area 4 and 8 was 1.48 C, but in egg-bearing time the difference was 2.5 months. However, comparing areas 4 and 15, the difference in temperature was 3.35 C but in egg-bearing time it was only half a month. As the temperature was lower and the ovigerous period longer, the proportion of mature females spawning during the same ovigerous period was found to decrease (Fig. 8). In the warmer inshore areas, areas 4 and 8, the spawning time is short, approximately one month. However in the offshore areas, areas 10 and 15, the spawning time is much less synchronized, spawning taking several months to reach a maximum. Moreover the proportion of egg-bearing females in the offshore areas never reached the almost 100% stage of all mature females having spawned during the same ovigerous period, as was seen in areas 4 and 8. In areas 4 and 8 most females were found to spawn for the first time at the age of 3 years, but in areas 10 and 15 at the age of 6 and 5 years respectively.

## DISCUSSION

The pattern of sexual maturation of *P. borealis* in inshore areas, that is the northwestern and northern fjords and the west coast shrimp grounds, is characterized by relatively low L50 values and estimations of age indicate that change of sex happens mostly when the shrimp is three years old. This is quite different from the offshore area where L50 is relatively high and estimations of age indicate females to be five or six years old when they spawn for the first time. The fjords at the north coast are geographically much closer to the offshore shrimp grounds than to the shrimp grounds at the west coast. However in the pattern of sexual maturation as well as other biological factors of *P. borealis*, the northern fjords are more similar to the west coast shrimp grounds than to the offshore areas.

The shrimp grounds at the west coast and the fjords differ from the offshore area in environmental features such as temperatures. The inshore areas, have considerably higher average annual near-bottom temperatures than offshore areas. This is well demonstrated in table 5, where results from areas 4 and 8 represent the inshore areas, and 10 and 15 the offshore areas. Figure 9 shows a general condition in near-bottom temperature around Iceland in late summer. The relatively warm water off the west coast is brought in by the Irminger current, flowing north along the west coast. This current then turns eastwards along the north coast, but in deeper areas cold arctic water is present at the bottom (Stefánsson 1962).

Environmental temperature has been found to affect the maturity of various marine invertebrates (Kinne 1979). Rasmussen (1953) found that at the coast of Norway, maturation of females of *P. borealis* occurred at a younger age in the southern areas compared to the northern areas. Appollonio *et al.* (1986) noted that changes in near-bottom temperature in the Gulf of Maine affected the rate of sex transition of *P. borealis* in the area and that in general the age at first spawning increased as the temperature decreased. Savard *et al.* (1989) and Savard and Parsons (1990) found that sex transition occurs earlier in the south than in the north of the West Atlantic. In the Gulf of Maine it occurred between ages three and four, but six and seven in the Davis Strait. Estrella and McKiernan (1989) found that size at maturity of female lobster (*Homarus americanus*) at the coast of Massachusetts was related to temperature. It is probable that temperature is the causative agent for considerable differences in L50 as well as other biological features of *P. borealis* between inshore and offshore areas in Icelandic waters. Also the variation in L50 within the offshore area seems to be related to temperature. The cold bottom water of areas 10 and 13 extends south into area 14 (Fig. 9), making L50 of area 14 resemble more the high L50s of areas 10 and 13 than those of its main adjacent areas 12 and 15. In the present study, the size at sex transition of *P. borealis* as well as age at sex change was found to differ between areas (Table 5). Although using somewhat different methods, Skúladóttir and Jónsson (1980) reached similar conclusions. This is controversial to the findings of Rasmussen (1953) who maintained that *P. borealis* changes sex at the same size but different age when looking at several stocks of *P. borealis* all the way from southern to northern Norway and Spitsbergen.

The great fall in L50 in area 4 from 1988 to 1989 can be attributed to an unusually large year-class from 1987. In 1989 a part of this year-class changed sex and matured as females only two years old, lowering the mean L50 from 19.13 to 16.40 mm. From 1985 to 1987 the stock density of *P. borealis* was low in area 4 (Skúladóttir *et al.* 1989). It is possible that the age at maturation of the 1987 year-class was affected by the low density of older shrimp. Charnov and Anderson (1989) found a positive correlation between L50 of *P. borealis* and the position of the overall size distribution of the breeding population. They considered this correlation as an evidence in support of the notion that year to year fluctuations in the population size distribution, probably caused mainly by a variation in recruitment, are tracked by year to year variation in the size at sex change. Present study seems to be a further indication of such phenotypic plasticity within a population of *P. borealis*. Changes in age and size at maturity that could be density dependent have been reported for various species of fish (Templeman and Bishop 1979; Beacham 1983). In fish, decline in age at maturity associated with decreased stock density has been attributed to increased growth rate, but the 1987 year-class of shrimp in area 4 seemed to be growing at an average rate.

The difference in maximum length of *P. borealis* between inshore and offshore areas is induced by differences in life-history factors such as growth-rate and age at maturity and as such is temperature related. The slow growing and late maturing shrimp in cold areas have

higher longevity and higher maximum length than the faster growing shrimp in warmer waters (Savard and Parsons, 1990). The mean max L of *P. borealis* seems to tie in with mean L50 as has been pointed out before (Skúladóttir 1990) when looking at all areas, i.e. the higher the L50 the higher the max L.

The ovigerous period of *P. borealis* has been found to vary with temperature and ranges from four and a half month to ten months (Shumway et al. 1985). This makes the egg-bearing time of ten months in area 10 among the longest on record. With that long ovigerous period it is unlikely that all *P. borealis* females are able to spawn each year. It seems likely that most will spawn every second year. This is substantiated by only very few females with headroes and eyed external eggs in the samples examined. There are all indications of the 20 to 30 % of mature females, that are not carrying eggs during the peak of the ovigerous period in offshore areas, being the last year's spawners. The egg-bearing part of the female population would then mostly be composed of first time spawners and older females not spawning the year before. As *P. borealis* in inshore areas spawn each year the question arises what effect this difference in reproduction strategy has on the population dynamics. Savard and Parsons (1990) pointed out that because females in higher latitudes (colder areas) are larger, fecundity is likely to increase in higher latitude and this could compensate for any loss from spawning every second year. Also if shrimp allocate less energy in reproduction, survival might be increased. The difference in mean lifetime egg production between populations from colder to warmer waters could then be reduced.

For area 8, hatching took place in less than one month, mostly in late April to the middle of May. In May there was very scanty information on the hatching of larvae in area 4, but in the last week of April, the hatching appeared to have just started. This agrees with Ástthórsson and Gíslason (1991) who systematically studied the occurrence of *P. borealis* larvae in this area in the year 1987. In their research the first very few larvae to appear in the planktonic stage were seen on the 25th of April and the bulk of the liberation seemed to take place between that date and the 13th of May. Sigurdsson and Hallgrímsson (1965) stated that in area 4, hatching took mainly place in March and April, which is about one month earlier than found in the present study. Skúladóttir *et al.* (1978) found that in spring 1977 hatching occurred earlier than in 1978, the 1978 results being close to that of the present study. In both those studies results were presented on an annual basis as compared to an average of several years as in the present study. Such long time average buffers the annual variations. As Ástthórsson and Gíslason (1991) pointed out that hatching was found to coincide with the spring bloom of phytoplankton. This agrees with the findings of Rasmussen (1953) in the many stocks observed in Norwegian waters. It is probably true for all inshore areas in Icelandic waters that hatching occurs near the time when the spring bloom reaches maximum. In an area where longer ovigerous period is needed for the development of the eggs, *P. borealis* would have to spawn earlier than in an area of short egg-bearing time, if the larvae are to be released at the phytoplankton bloom. This is actually what was found when areas 4 and 8 were compared. The synchronized spawning and later hatching of larvae in inshore areas is probably induced by seasonal changes in the environment. However, in the offshore area such changes are much less pronounced and spawning as well as hatching extends over a period of at least two months.

Distinct difference in maturity pattern, L50 and maximum length of *P. borealis* between inshore and offshore areas should make migration of large shrimp noticeable. Presence of unusually large females or males has not been observed in the fjords at the northwest and north coast or in the inshore areas at West Iceland. Migration of inshore shrimp to offshore areas is more likely to go unnoticed as in such a case the inshore population would probably become spread over a large area. However, changes in population size of *P. borealis* in inshore areas have so far not indicated offshore movement on a large scale. This does not exclude the possibility of transport of larvae or juvenile shrimp between inshore and offshore grounds. In the offshore area larval as well as young *P. borealis* will probably drift by ocean currents flowing from west to east. It is possible however that the difference in proportion of mature females between areas 10 and 13 and 15-17 is caused by migration of shrimp back from east to west.

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## REFERENCES

- Allen, J. A. 1959.** On the biology of *Pandalus borealis* Krøyer, with reference to a population off the Northumberland coast. J. Mar. Assoc. U. K. **38**. 189-220.
- Appollonio, S., D. K. Stevenson and E. E. Dunton, Jr. 1986.** Effects of temperature on the biology of the northern shrimp, *Pandalus borealis* in the Gulf of Maine. NOAA Tech. Rep. NMFS **42**, 22pp.
- Ástthórsson Ó. S. and A. Gíslason 1991.** Seasonal abundance and distribution of Caridea larvae in Ísafjörð-deep, North-west Iceland. J. Plankton. Res. **13**. 91-102.
- Beacham, T. D. 1983.** Variability in median size and age at sexual maturity of Atlantic cod, *Gadus Morhua*, On the Scotian shelf in the northwest Atlantic ocean. Fish. Bull. **81** No 2. 303-321.
- Charnov, E. L. and P. J. Anderson 1989.** Sex change and population fluctuations in pandalid shrimp. Am. Nat. **134**. 824-827.
- Estrella, B. T. and D. J. McKiernan 1989.** Catch-per-unit-effort and biological parameters from the Massachusetts coastal lobster (*Homarus americanus*). Resource: Description and trends. NOAA Technical Report NMFS **81**. 21 pp.
- Fox, W. W. 1972.** Dynamics of exploited pandalid shrimps and an evaluation of management models. Ph. D. Thesis. Univ. Washington, Seattle. 193 pp.
- Kinne, O. 1970.** Temperature: animals-invertebrates. Pages 407-514 in O. Kinne, ed. Marine ecology, Vol 1, Environmental factors, Pt. 1. Wiley-Interscience, London.
- McCrary, J. A. 1971.** Sternal spines as a characteristic for differentiating between females of some Pandalidae. J. Fish. Res. Board Can. **28**. 98-100.
- MacDonald P.D.M. and T. J. Pitcher 1979.** Age-groups from size-frequency data: A versatile and efficient method of analysing distribution mixtures. J Fish. Res. Board Can. **36**. 987-1011.
- Rasmussen, B. 1953.** On the geographical variation in growth and sexual development of the deep sea prawn (*Pandalus borealis* Kr.). Fiskeridir. Skr. Havunders. (Rep. Norw. Fish. Invest.) **10** (3). 160 pp.
- Savard, L., D. Parsons and D. M. Carlsson 1989.** Age and growth of northern shrimp (*Pandalus borealis*) in Davis Strait (NAFO SA 0-1). NAFO SCR Doc. 89/94. Ser. No. N1694 14pp. (Mimeo).
- Savard, L. and D. Parsons 1990.** Geographic variation in the life history of *Pandalus borealis* from the Northwest Atlantic. ICES symposium on shellfish life histories and shellfishery models, held in Moncton 1990. No. 27. 4 pp (mimeo)
- Shumway, S. E., H.C. Perkins, D. F. Schick and A.P. Stickney 1985.** Synopsis of biological data on the pink shrimp *Pandalus borealis* Krøyer, 1938. NOAA Technical report NMFS **30**. 57 pp.
- Sigurdsson, A. and I. Hallgrímsson 1965.** The deep-sea prawn (*Pandalus borealis*) in Icelandic waters. Rapp. P.-V. Réun. Cons. Int. Explor. Mer. **156**. 105-108.
- Skúladóttir, U. 1990.** Defining stocks of *Pandalus borealis* off Northern Iceland using the maximum length and maturity ogive as a measure. ICES symposium on shellfish life histories and shellfishery models, held in Moncton 1990. No. 95. 15 pp. (Mimeo).
- Skúladóttir, U., G. S. Bragason and V. Helgason 1989.** The stock size of *Pandalus borealis* in Ísafjörðardjúp, estimated by VPA and Area swept. NAFO SCR doc 89/96. Serial No. N1698. 18 pp. (Mimeo).
- Skúladóttir, U., E. Jónsson and I. Hallgrímsson 1978.** Testing for heterogeneity of *Pandalus borealis* populations at Iceland. ICES, C.M. 1978/K:27. 43 pp. (Mimeo).
- Skúladóttir, U. and E. Jónsson 1980.** Rækjan við Ísland Ægir, **73**, 2. 86-96. (In Icelandic).
- Stefánsson, U. 1962.** North Icelandic water. Rit Fiskideildar **3**. 269 pp.
- Stefánsson, U. and S. Jónsdóttir 1974.** Near-bottom temperature around Iceland. Rit Fiskideildar V. bd. **5**. 73 pp.
- Templeman, W., and C. A. Bishop 1979.** Sexual maturity and spawning in haddock, *Melanogrammus aeglefinus*, of St. Pierre bank. Int. Comm. Northwest Atl. Fish Res. Bull. **14**. 77-83.





Table 1. Sampling areas, time in the year, number of samples, total number of *P. borealis* measured and the percentage of mature females by area in 1988.

Area	Area No.	Sampling time	No. of samples	Total No. measured	% mature females
Eldey	1	Aug	4	406	7.7
Arnarfjörður	3	Okt	20	2626	45.5
Ísafjardardjúp	4	Okt	47	10600	26.9
Húnaflói	5	Okt	24	4205	17.6
Skagafjörður	6	Okt	23	2976	22.4
Axarfjörður	7	Okt-Nov	12	1382	11.9
Snæfellsnes	8	Jun-Aug	6	1693	33.9
Denmark Strait	9	Aug-Sep	6	484	73.6
Nordurkantur	10	Jul-Aug	50	7122	23.2
Spordagrunn	11	Jul	13	2010	24.5
Skagafjardardjúp	12	Jul	11	1739	23.2
Kolbeinsey	13	Jul-Aug	32	4660	22.2
Eyjafjardaráll	14	Jul-Aug	8	1107	31.2
Grímsey	15	Aug	14	2856	15.8
Sléttugrunn	16	Aug	21	3941	12.1
Langesdjúp	17	Sep	11	2173	6.4
Bakkaflóadjúp	18	Sep	6	971	10.1
Héradsdjúp	19	Sep	14	2638	14.3

Table 2. Sampling areas, time in the year, number of samples, total number of *P. borealis* measured and the percentage of mature females by area in 1989.

Area	Area No.	Sampling time	No. of samples	Total No. measured	% mature females
Eldey	1	Aug-Sep	12	2256	26.1
Arnarfjörður	3	Okt	16	2939	36.1
Ísafjardardjúp	4	Okt	45	8167	27.9
Húnaflói	5	Okt	29	4037	13.9
Skagafjörður	6	Sep	15	2272	33.1
Axarfjörður	7	Sep	12	1783	29.4
Snæfellsnes	8	Jul-Aug	7	1343	31.2
Nordurkantur	10	Jun-Jul	42	6599	25.6
Spordagrunn	11	Jun	12	2080	19.9
Skagafjardardjúp	12	Jul	10	1655	14.5
Kolbeinsey	13	Jun-Jul	27	4330	21.0
Eyjafjardaráll	14	Jun-jul	6	1052	12.9
Grímsey	15	Jul	13	2545	12.8
Sléttugrunn	16	Jul	18	3277	9.2
Langesdjúp	17	Jul	7	1333	11.2
Bakkaflóadjúp	18	Jul	5	1220	10.1
Héradsdjúp	19	Jul	13	2996	13.0
Tangaflak	20	Jul-Aug	8	1902	35.6

Table 3. The average L50 for each area in 1988 and 1989 and the respective SE. In the calculations of mean L50 only those samples were included where the fit of a simple line to the data was significant at the 0.05 level.

Area No.		No. of Samples	1988		No. of Samples	1989	
			Mean L50	SE of L50		Mean L50	SE of L50
1	Inshore	3	20.71	0.20	12	19.54	0.15
3	"	20	19.24	0.14	15	19.84	0.13
4	"	39	19.13	0.07	45	16.40	0.07
5	"	18	17.69	0.09	21	17.55	0.18
6	"	18	17.02	0.10	14	16.92	0.08
7	"	8	18.08	0.24	6	19.64	0.84
8	"	6	19.63	0.18	7	20.01	0.41
9	Offshore	5	28.09	0.24	-	-	-
10	"	50	23.67	0.10	42	24.92	0.15
11	"	13	22.68	0.26	12	23.58	0.34
12	"	11	22.49	0.13	10	23.45	0.46
13	"	33	23.83	0.12	27	24.81	0.13
14	"	8	23.60	0.23	6	24.20	0.34
15	"	14	21.69	0.15	13	22.32	0.24
16	"	19	22.06	0.16	18	22.63	0.15
17	"	10	22.16	0.22	7	22.55	0.22
18	"	5	21.69	0.22	4	22.61	0.21
19	"	13	21.30	0.13	12	22.31	0.21
20	"	-	-	-	8	23.80	0.21

Table 4. The average max L for each area in 1988 and 1989 and the respective SE.

Area No.		No. of Samples	1988		No. of Samples	1989	
			Mean max L	SE of max L		Mean max L	SE of max L
1	Inshore	4	23.50	0.74	12	23.42	0.29
3	"	20	25.50	0.40	16	24.13	0.33
4	"	47	23.46	0.26	45	22.70	0.21
5	"	24	22.46	0.34	29	22.00	0.38
6	"	23	20.94	0.24	15	21.33	0.39
7	"	12	21.88	0.51	12	23.75	0.43
8	"	6	24.33	0.31	7	24.71	0.34
9	Offshore	6	34.42	0.27	-	-	-
10	"	50	28.18	0.19	42	28.98	0.16
11	"	13	28.00	0.44	12	29.25	0.56
12	"	11	27.73	0.68	10	27.90	0.73
13	"	32	28.45	0.19	27	29.04	0.20
14	"	8	29.06	0.43	6	29.42	0.61
15	"	14	27.82	0.63	13	28.89	0.34
16	"	21	27.10	0.36	18	27.17	0.40
17	"	11	26.17	0.53	7	28.93	0.44
18	"	6	28.75	1.13	5	27.80	0.86
19	"	14	27.50	0.50	13	28.31	0.41
20	"	-	-	-	8	29.56	0.41

Table 5. Age at first spawning as female, length of egg-bearing time and L50 for *P. borealis* in four different areas and the average annual near-bottom temperature in each area. Length of each egg-bearing time is an average for the years 1983-1990 (areas 10 and 15) and 1982-1990 (areas 4 and 8) with additional data from 1973-1980 for area 8. The average annual near-bottom temperature was calculated for the period 1974-1989. The mean depth stated is that of hydrographic stations used for calculation of the average annual near-bottom temperature in each area.

Area	Area No.	1988		1989		Egg-bearing months	Temperature C	Mean depth m
		Mean L50 mm	Age at 1st spawn.	Mean L50 mm	Age at 1st spawn.			
Snæfellsnes	8	19.6	3	20.0	3	5.5	5.98	225
Ísafjardardjúp	4	19.1	3	16.4	2 and 3	8.0	4.50	80
Grimsey	15	21.7	5	22.3	5	8.5	1.15	350
Nordurkantur	10	23.7	6	24.9	6	10.0	-0.01	400

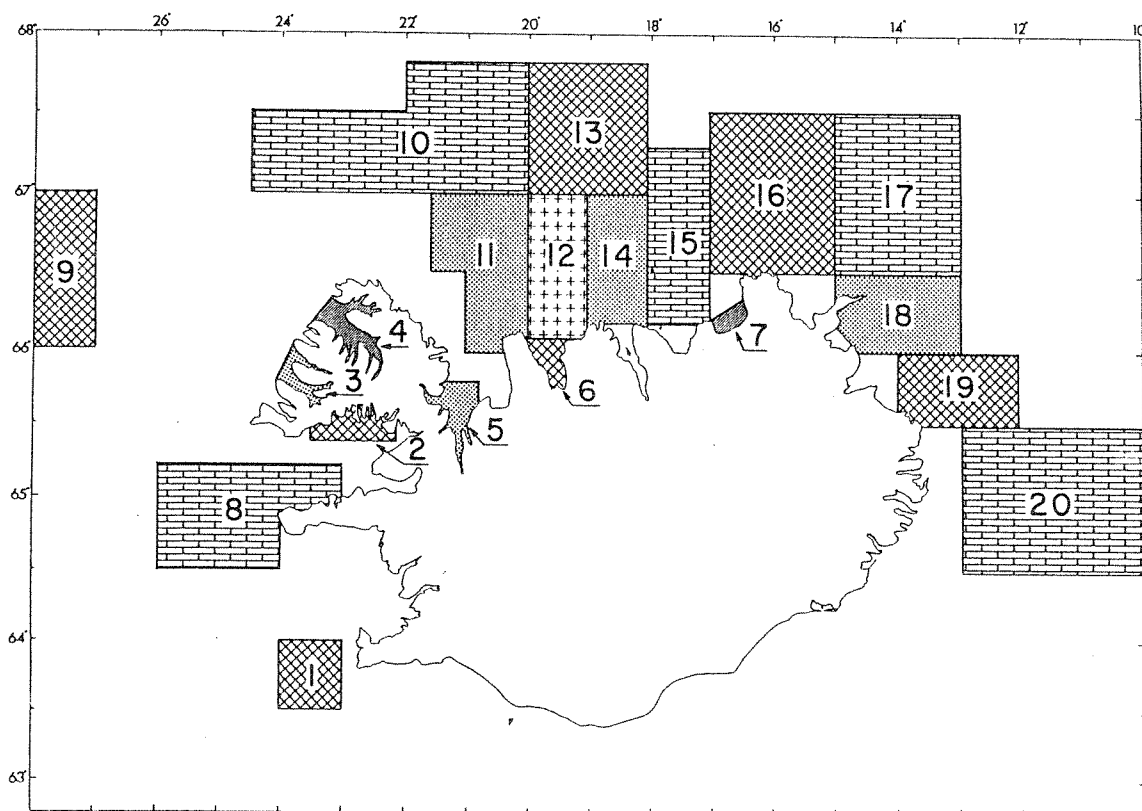


Figure 1. The main shrimp areas in Icelandic waters. Areas 1-7 : Inshore areas, depth usually between 50 and 150 m. Area 8 : Resembles the inshore areas but average depth just over 200 m. Areas 9-20 : Offshore areas, depth greater than 200 m.

Inshore	No.	Offshore	No.
Eldey	1	Denmark Strait	9
Arnarfjörður	3	Nordurkantur	10
Ísafjardardjúp	4	Spordagrunn	11
Húnaflói	5	Skagafjardardjúp	12
Skagafjörður	6	Kolbeinsey	13
Axarfjörður	7	Eyjafjardaráll	14
Snæfellsnes	8	Grimsey	15
		Sléttugrunn	16
		Langanesdjúp	17
		Bakkaflóadjúp	18
		Héraðsdjúp	19
		Tangaflak	20

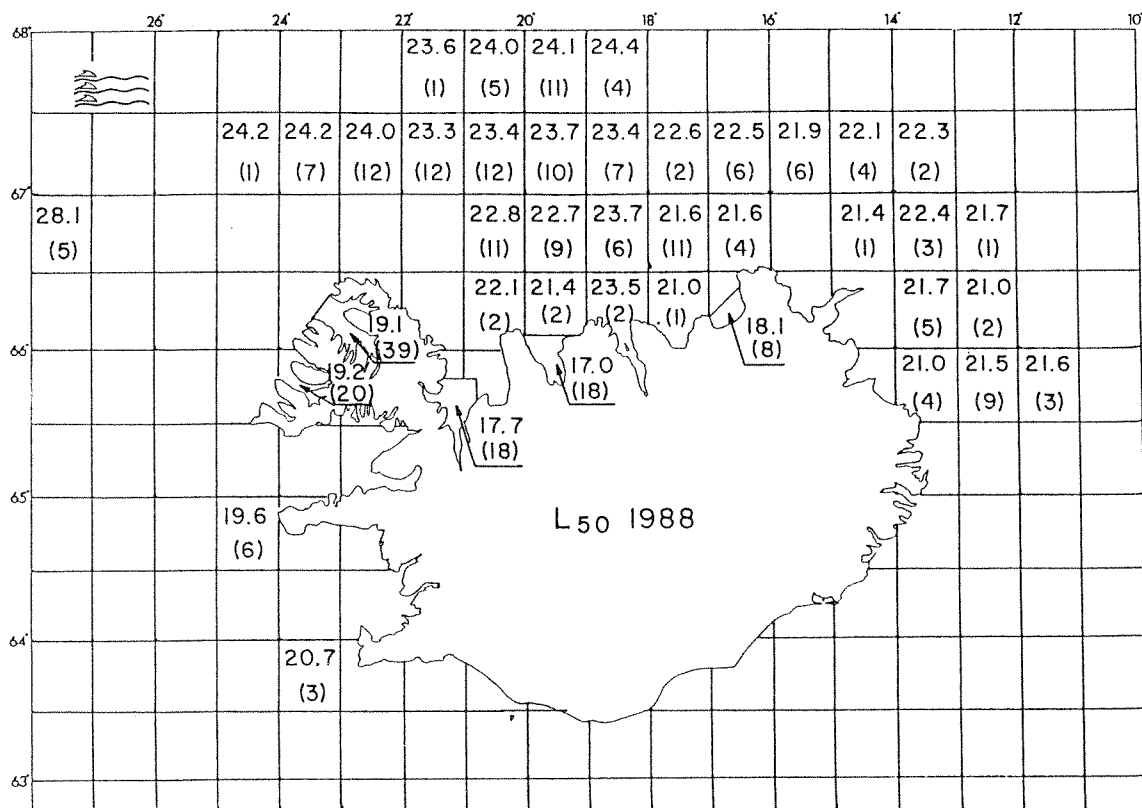


Figure 2. Mean L<sub>50</sub> by unit areas and fjords in 1988. Number of samples in brackets.

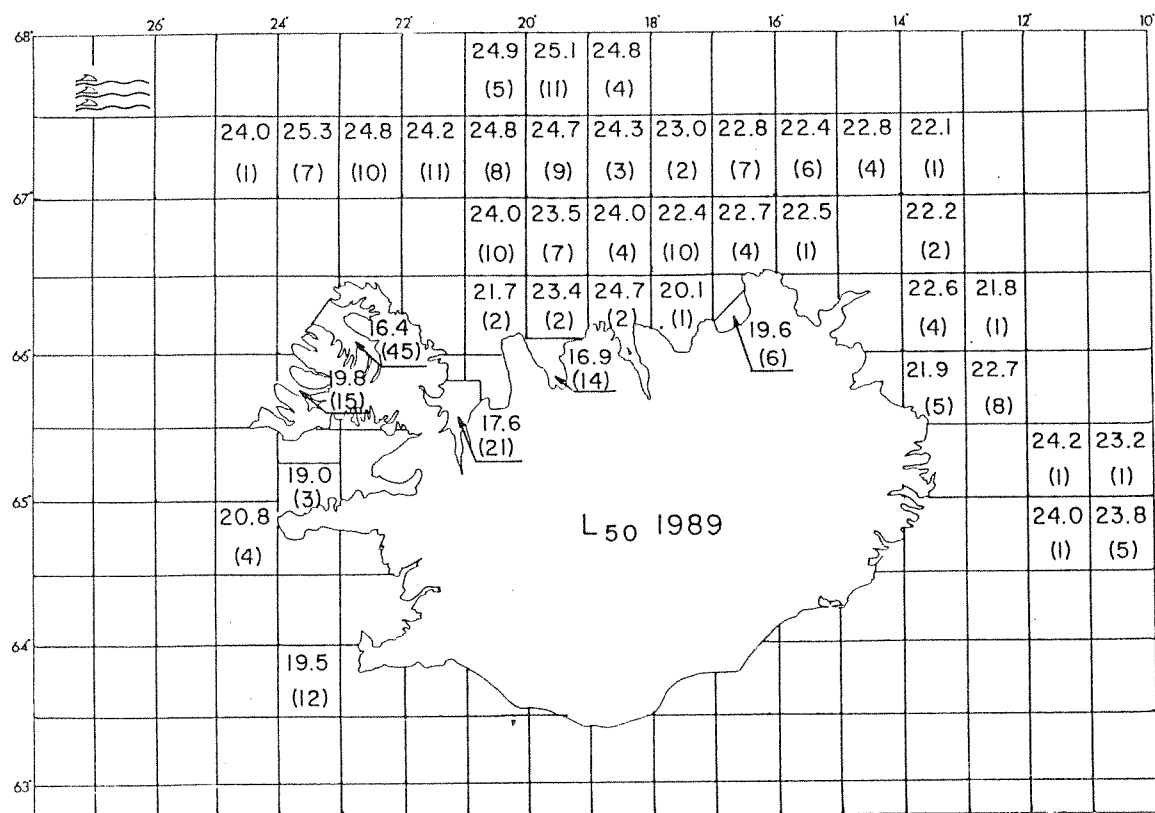


Figure 3. Mean L<sub>50</sub> by unit areas and fjords in 1989. Number of samples in brackets.

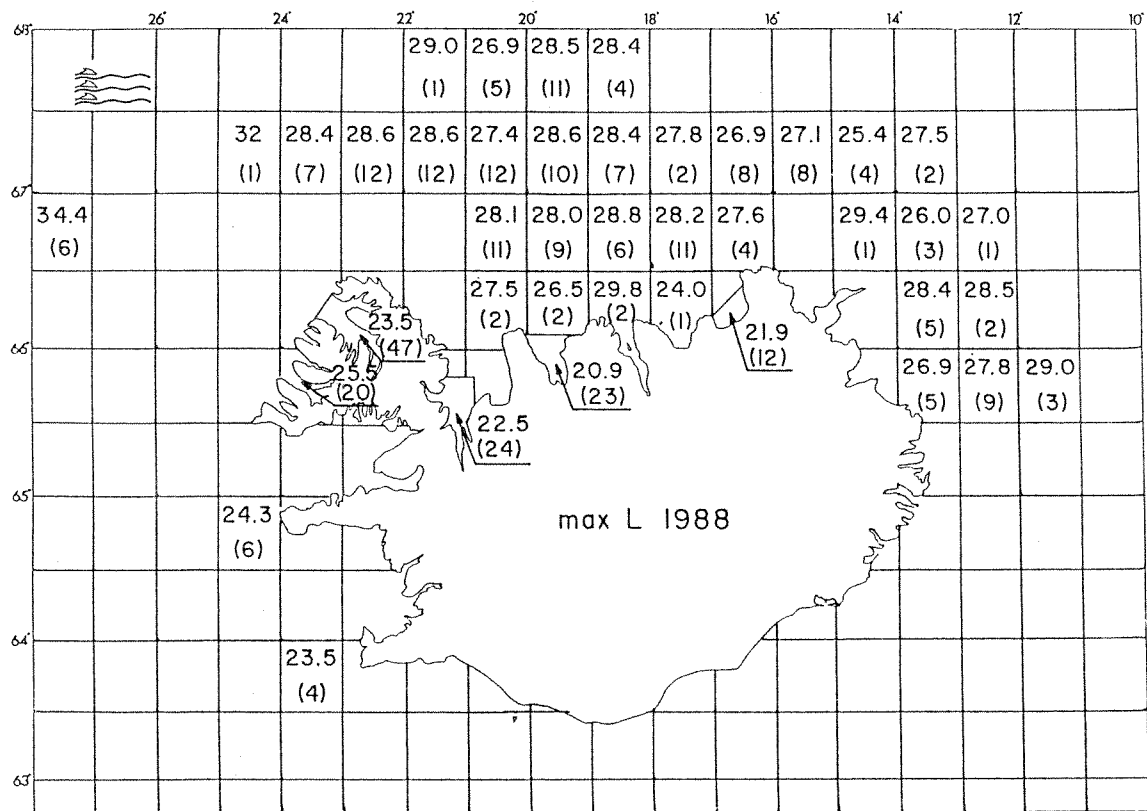


Figure 4. Mean max L by unit areas and fjords in 1988. Number of samples in brackets.

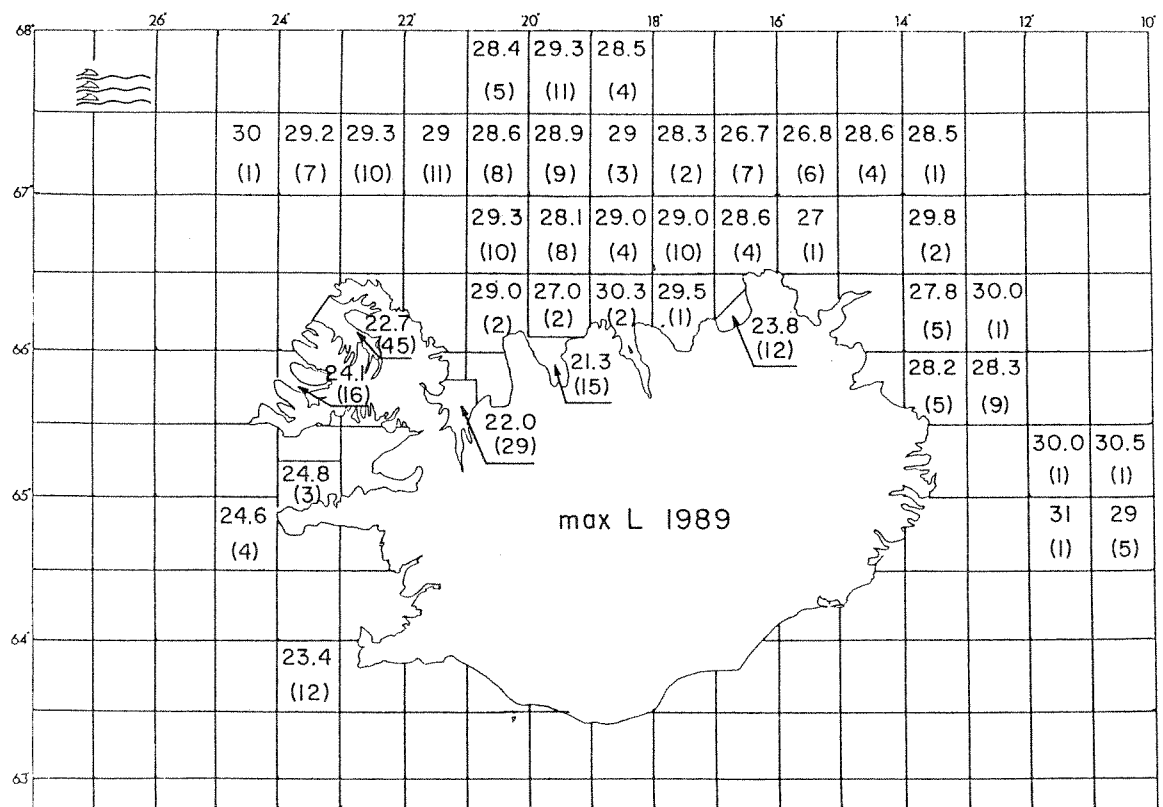


Figure 5. Mean max L by unit areas and fjords in 1989. Number of samples in brackets.

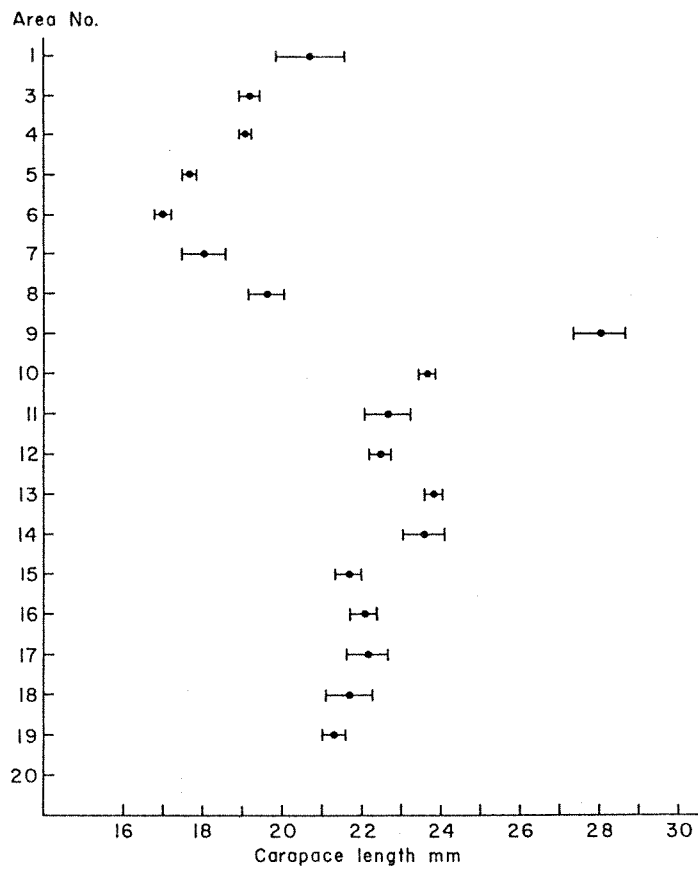


Figure 6. The mean L50 and 95% confidence limits by areas in 1988.

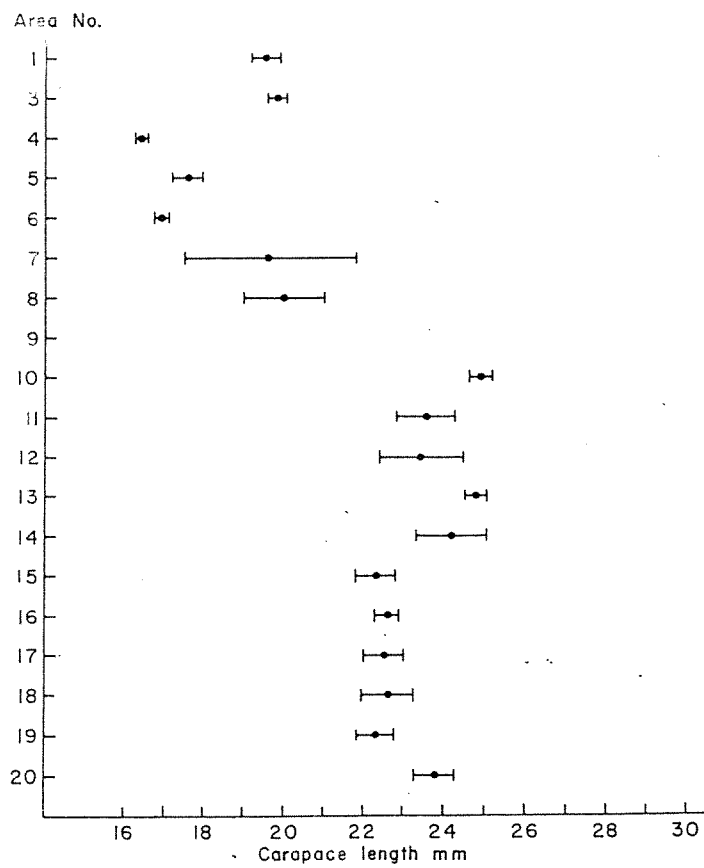


Figure 7. The mean L50 and 95% confidence limits by areas in 1989.



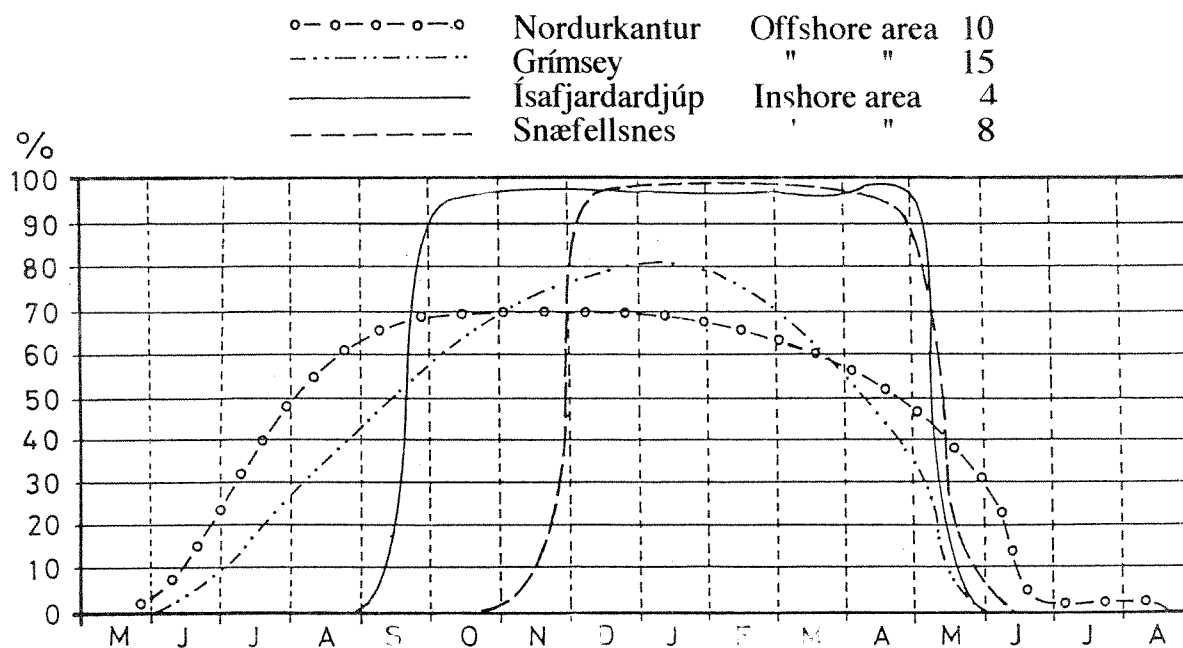


Figure 8. Ovigerous periods of *P. borealis* in four areas in Icelandic waters. Egg-bearing females as a percentage of all mature females and maturing females preparing to spawn during the same ovigerous period.

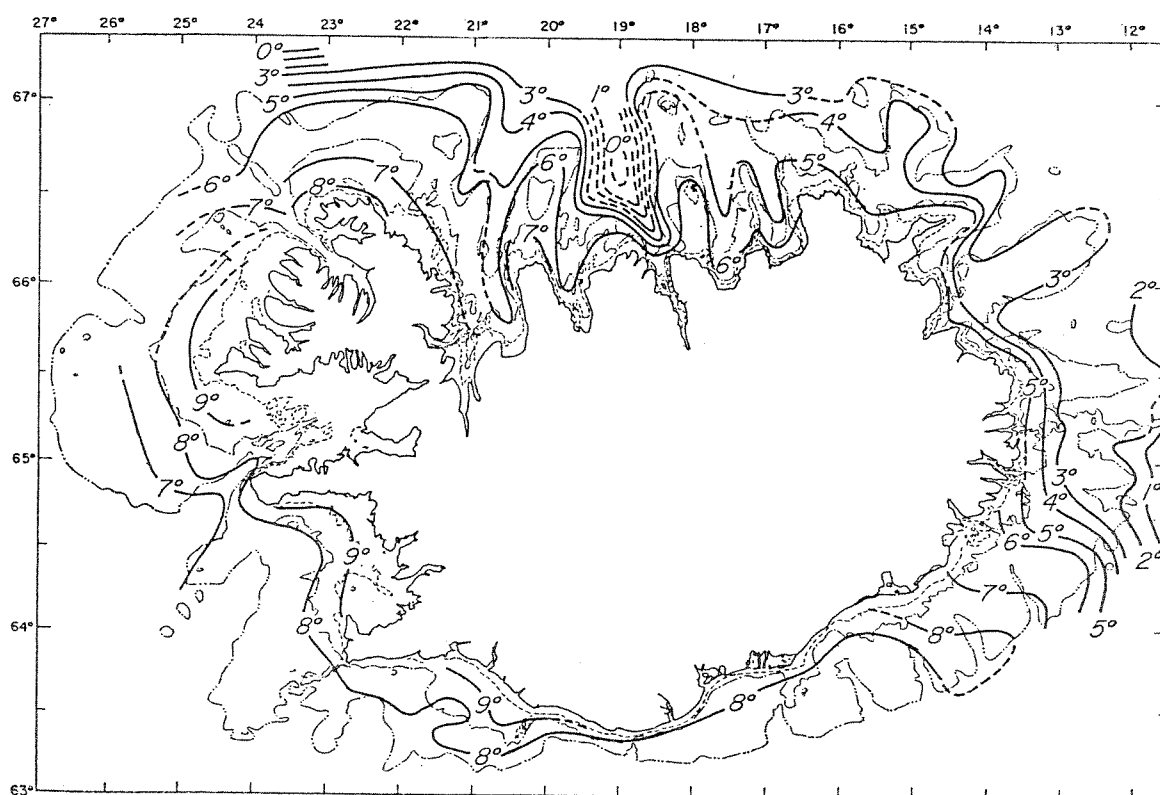


Figure 9. Near-bottom temperature, an average of the years 1948-1973 around Iceland in August. From Stefánsson and Jónsdóttir (1974) with the courtesy of the authors.