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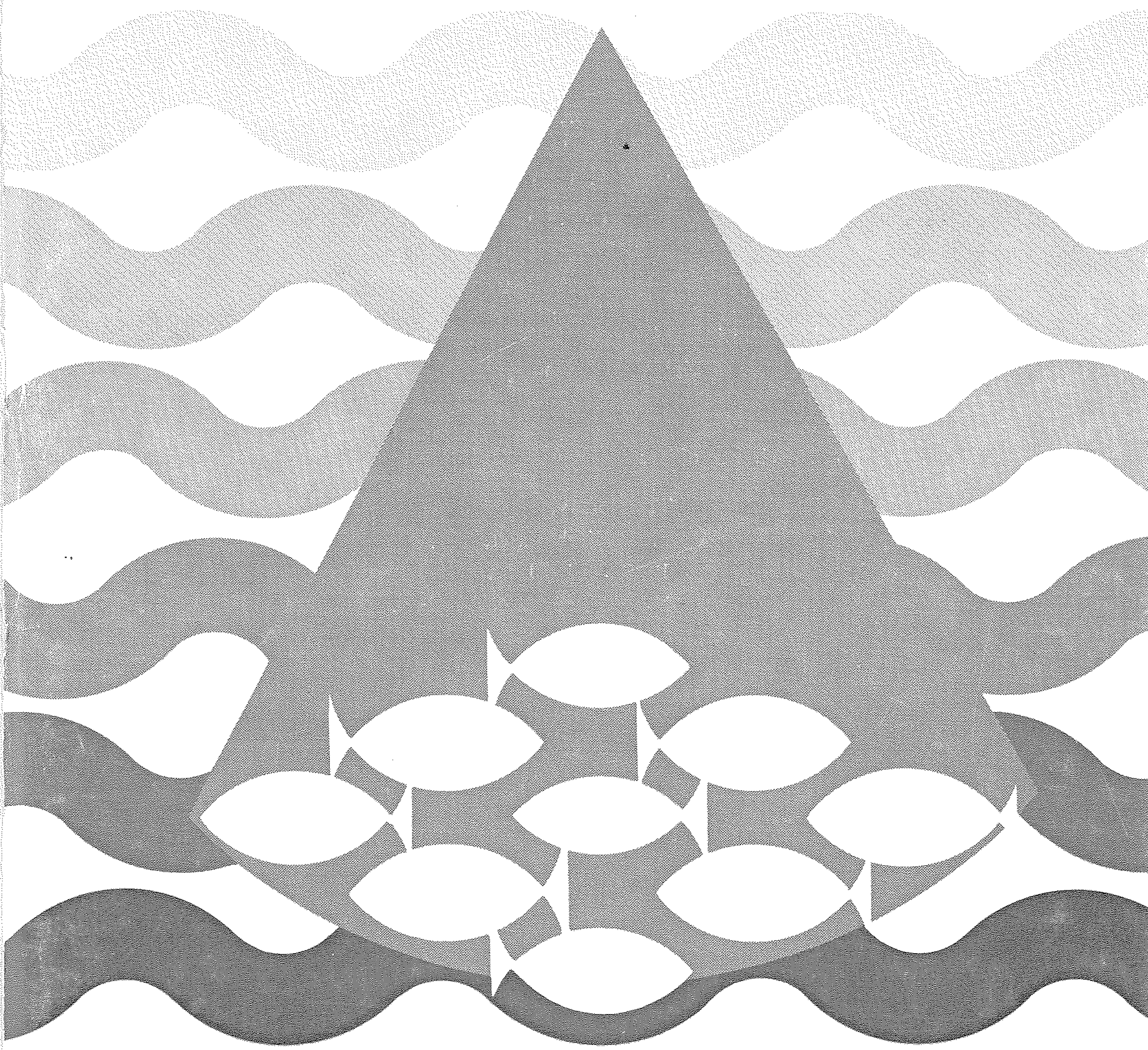

DIRECTORATE OF FISHERIES, BERGEN, NORWAY
1983

FiskDir. Skr. Ser. HavUnders., 17: 377–430.

POPULATIONS OF THE DEEP-SEA SHRIMP (*PANDALUS BOREALIS* KRØYER) IN THE BARENTS SEA

By

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CONTENTS

ABSTRACT

TEIGSMARK, G. 1983. Populations of the deep-sea shrimp (*Pandalus borealis* Krøyer) in the Barents Sea. *FiskDir. Skr. Ser. HavUnders., 17:* 377–430.

Three populations of *P. borealis* were identified in the open part of the Barents Sea. In the (4–1) population the females spawn each year and sex-change occurs 4 years old. This population was found in the southwestern part of the sea and mostly in water masses with a temperature of approximately 2°C. In both the (5–2) and (6–2) populations the females spawn biennially, and in these populations sex-change takes place 5 and 6 years old respectively. The (5–2) population was found in the central part of the sea in water masses with a temperature a little below 1°C, while the (6–2) population was found in the northern part of the ocean in water masses with a temperature a little above 0°C.

Von Bertalanffy growth curves, total mortality estimates and estimates of maximum age are given for each population. The (4–1) population, having the fastest growth, had the highest total mortality and the shortest lifespan, while the very slow-growing (6–2) population had the lowest total mortality and attained the highest age.

Egg hatching was found to take place in May. The (4–1) population spawns markedly later than the two other populations, and the duration of the egg-carrying period is therefore regulated mainly by differences in the time of spawning. Length-fecundity relationships are given for the populations.

Vertical migration was observed to take place over a depth interval of more than 300 meters. The youngest individuals participated in this migration to the greatest extent. A horizontal migration of the (4–1) population, probably caused by changes in the hydrographical conditions, is described.

A grand total of 0.2% of the individuals were infected by the bopyride isopode *Phryxus abdominalis* (Krøyer).

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GENERAL INTRODUCTION

The Norwegian trawl fishery for deep-sea shrimps (*Pandalus borealis* Krøyer) started in Oslofjorden in 1898. In the succeeding decades the shrimp fishery expanded northwards along the Norwegian coast as new shrimp fishing grounds were discovered, and this lead to a steady increase in the yearly catch (Fig. 1). In northern Norway the fishery for shrimps started a few years before the second world war, and in the mid 1950's an economically significant fishery for shrimps took place all along the Norwegian coastline. Until 1970, the Norwegian shrimp fishery was confined to coastal areas and fjords and was carried out with rather small vessels. There were then no prospects for further expansion of this fishery.

In 1970, however, large shrimp fields were discovered in the open part of the Barents Sea (RASMUSSEN and ØYNES 1970), and within a few years a significant fishery had developed in this area. In 1972, Norwegian fishermen, mainly from the Møre District, began to trawl for shrimps in the waters off West Greenland. The development of this offshore fishery lead to a large increase in the yearly catch (Fig. 1). It also brought about great changes in the structure of the shrimp fishing fleet, especially in northern Norway, where the fleet is now mainly composed of large ocean-going vessels.

The main fishing grounds in the Barents Sea are at Nordkappleira, Tiddly-Banken, Thor Iversen-Banken, Gåsbanken and in the deep water areas between Hopen and Sentralbanken (Fig. 2). Economically the deep-sea shrimp is today the fourth most important species for Norwegian fisherman, and the Barents Sea area yields a large part of the yearly catch.

In his work on the biology of *P. borealis* in Norwegian waters, RASMUSSEN (1953) did not treat the open part of the Barents Sea. Some USSR scientists have, however, published information on this subject (PALENICHKO 1941, BRYAZGIN 1970, 1973, BARENBOIM 1978). The aim of the present study is to investigate further the biology of *P. borealis* in the open part of the Barents Sea. The paper is divided into two parts. In Part I stock structure is investigated, and in Part II the identified populations are further characterized biologically with emphasis on growth, mortality and reproduction.

Spitsbergen waters are not included in the present study.

MATERIALS AND METHODS

This section includes information about the materials on which this work is based, and also about methods of a more general character, i.e., with reference to both Part I and Part II. Other methods with reference to just one part will be described in the appropriate part.

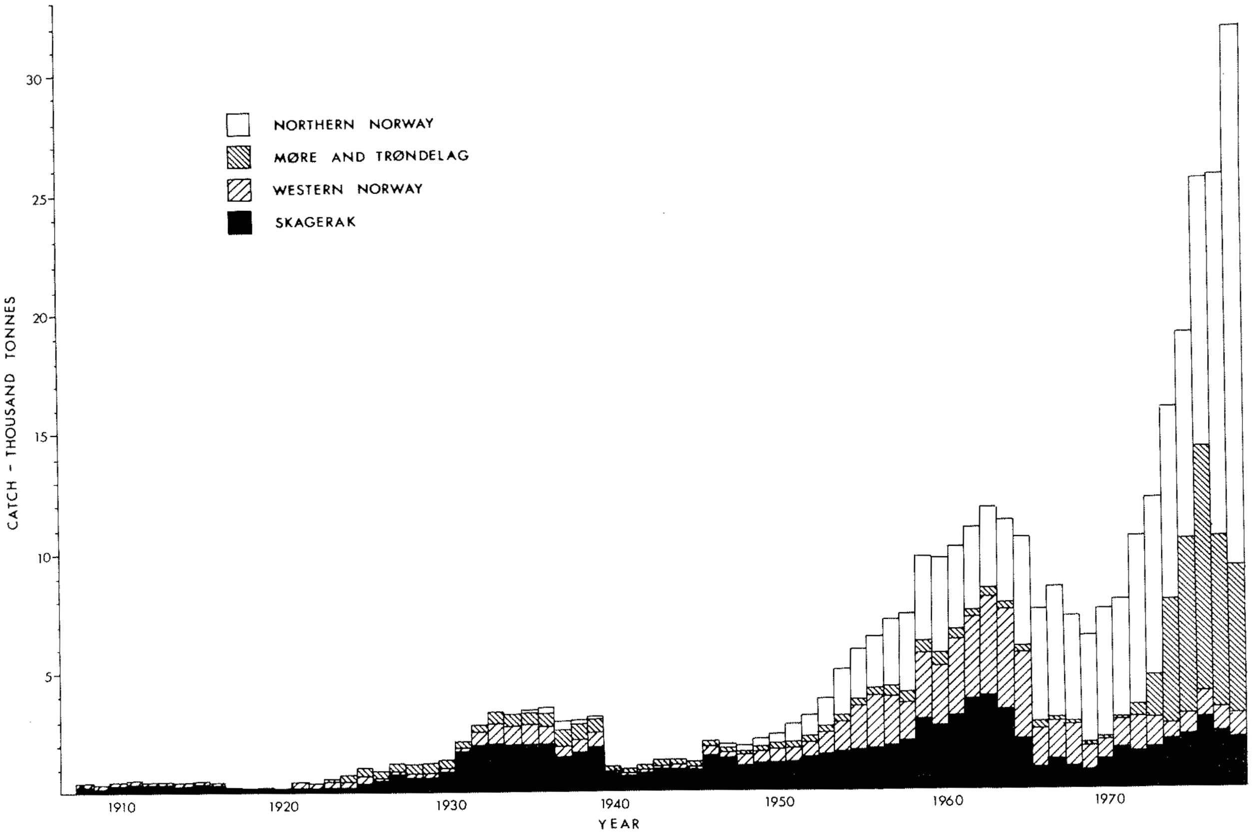

Fig. 1. Norwegian catch of deep-sea shrimp from 1908 to 1978, divided according to region where landed.

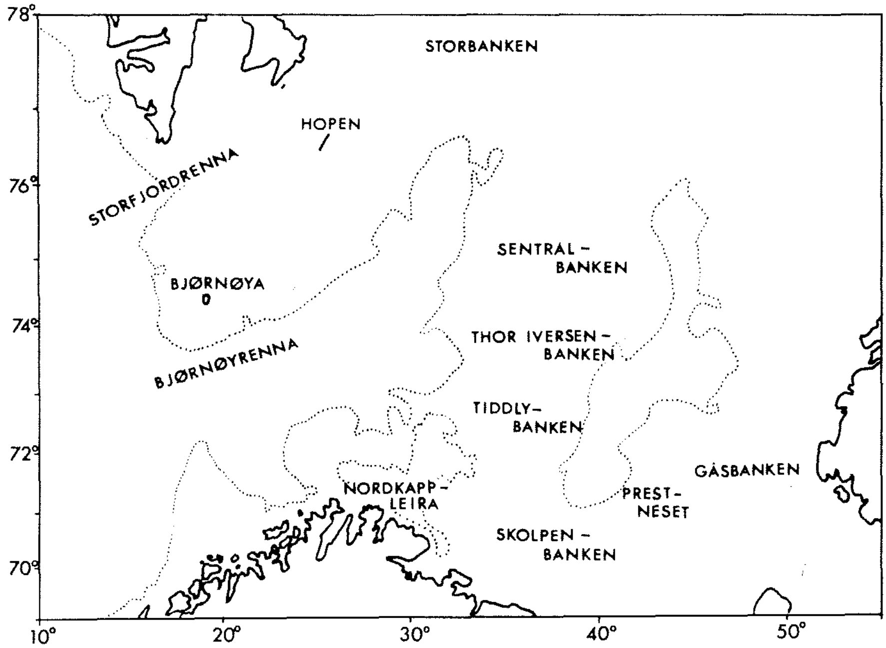

Fig. 2. Geographical names referred to in the text.

SOME DEFINITIONS AND SYMBOLS

$\mu(j,k)$: Mean value in the length distribution of yearclass j on station number k.

$\sigma(j,k)$: Standard deviation in the length distribution of yearclass j on station number k.

$N(j,k)$: Number of individuals in yearclass j on station number k.

l: Length, in millimeters. Used on carapace length as defined in ANON. (1972).

w: Weight, in g.

SAMPLES

The material consists of 78 samples taken by bottom trawl in 1978 and 1979 and 8 samples taken by pelagic trawl in 1978 (Table 1). More detailed information about the separate samples is given in Table I. The samples were collected during fish and shrimp surveys by ships of the Institute of Marine Research, Bergen.

Most samples taken with bottom trawl were used to identify the populations and to study growth and mortality. Some samples were used only to investigate spawning and hatching times. The pelagic trawl samples give information about vertical migration.

Table 1. Analysed samples.

Ship	Time	Number of samples	Cruise designation
Samples used to identify the populations.			
R/V «G. O. Sars»	2/2–3/3 1978	9	Cruise 1–78
R/V «G. O. Sars»	20–22/4 1978	2	Cruise 2–78
M/S «Børvåg»	4/5–14/6 1978	22	Cruise 3–78
R/V «G. O. Sars»	23–26/6 1978	2	Cruise 4–78
R/V «G. O. Sars»	1/9 1978	1	Cruise 5–78
R/V «G. O. Sars»	23/1–2/3 1979	11	Cruise 1–79
M/S «Stadhav»	12–23/6 1979	19	Cruise 3–79
Samples used to investigate spawning and hatching times.			
M/S «Finnmarkværing»	20–23/10 1978	4	Cruise 6–78
M/S «Stadhav»	10–22/5 1979	7	Cruise 2–79
R/V «G. O. Sars»	15/7 1979	1	Cruise 4–79
Pelagic samples.			
R/V «G. O. Sars»	6–11/2 1978	2	
R/V «Johan Hjort»	20/9 1978	1	
R/V «G. O. Sars	22/9–2/10 1978	5	

SAMPLING GEAR

Detailed information about the sampling gear on each station is given in Table I. In most hauls, shrimp trawls with a mesh size of 35 mm were used. In some of these hauls a fine-meshed net (18 mm) was used in the cod end. On R.V. "G.O. Sars" in 1978 a Granton bottom trawl was used with a 22 mm net in the cod end. The pelagic samples were taken with a pelagic trawl with a mesh size of 4 mm.

The selection factor (SF) for *P. borealis* has been calculated to be 0.436 (ANON. 1977). By using $l_{c50\%} = SF \cdot$ mesh size in the trawl, the following $l_{c50\%}$-values are found:

Mesh size	$l_{c50\%}$
35 mm	15.3 mm
22 mm	9.6 mm
18 mm	7.9 mm

In THOMASSEN and ULLTANG (1975) it is shown that the width of the selection curve becomes smaller with decreasing mesh size. In hauls where a fine-meshed net (18 mm or 22 mm) was used, very few individuals smaller than $l_{c50\%}$ were captured. It is therefore unnecessary to adjust for the selection of the gear in these situations. However, for samples taken with a 35 mm trawl it is necessary to carry out such adjustments. A selection curve for the 35 mm trawl, based on the form of that for the 36 mm trawl (THOMASSEN and ULLTANG 1975), but with $l_{c50\%}$ equal to 15.3 mm, was constructed (Fig. 3).

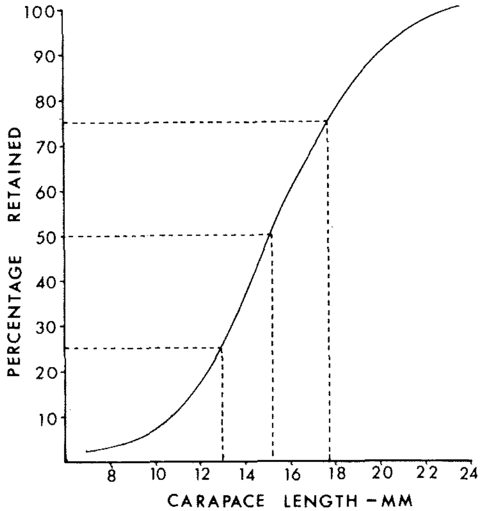

Fig. 3. Constructed selection curve for a shrimp trawl with mesh size 35 mm.

SAMPLE SIZE

In each sample many parameters are to be estimated, and no single one of them can be selected to estimate sample size. In ANON. (1972) it is recommended that a sample size of more than 2000 individuals be used if the length distribution is to be split into year classes. It is clear that if such a large sample size should be used, few samples could be examined. It was therefore decided to use practical experience in determining sample size. More than 1100 individuals were examined from one station, and the various parameters were then estimated for sample sizes up to this level. Good agreement was found with the final results when using 300–500 specimens. A sample of this size was therefore used whenever possible.

PRESERVATION

Only a few samples could be examined at sea, and therefore most samples were frozen and later examined on land. For thawing, the frozen sample was placed in fresh water.

Freezing was not found to have any significant effect on either the length or weight of the shrimp. It is surprising that no effect was found on weight, but due to lack of fresh material, the experiment could not be repeated.

LENGTH MEASUREMENT

Carapace length was measured from the back of the eye socket to the mid dorsal point of the posterior margin of the carapace (ANON. 1972). The shrimps were preferably measured on the left side of the carapace. A caliper was used, and all lengths were measured to the nearest 0.1 mm below.

HORSTED and SMIDT (1956) measured the carapace length from the back of the eye socket to the posterior, lateral margin of the carapace. If this latter length is designated CL′ and the above mentioned length is designated CL, the following relationships are found:

$$\begin{aligned} CL &= 0.868 \cdot CL' + 0.100 \\ CL' &= 1.149 \cdot CL - 0.050 \end{aligned} \quad (r^2 = 0.99, N = 225)$$

When it was impossible to measure CL, it was calculated by measuring CL′ and using the above relationship.

After measurement, the shrimps were grouped in length intervals of 0.5 mm, based on sex and reproductive stage. Length groups with an interval of 1.0 mm were used when splitting the length distribution into normally distributed components corresponding to year classes.

WEIGHING

Shrimps to be weighed were placed in fresh water. After approximately one-half hour they were taken out of the water. A pellicle under the carapace was punctured because water was often found there. They were then air-dried for a few minutes. All weights were rounded downwards to the nearest 0.1 g.

DETERMINATION OF SEX AND REPRODUCTIVE STAGE

Determination of sex was based on the form of the endopodite of the first pleopod as described by RASMUSSEN (1953).

Females and intersexes (individuals changing sex) were classified into several reproductive stages by use of the following scheme:

1) *Ovigerous females, eyes not visible on the eggs (BR−Ø).*
   This stage includes females with newly spawned eggs. These eggs are smaller than eggs with visible eyes and have a distinct, green colour.

2) *Ovigerous females, eyes visible on the eggs (BR+Ø).*
   This stage includes females with older eggs. The eggs have now lost their distinct, green colour and are larger than the eggs without visible eyes.

3) *Females with setae on the pleopods (JH).*
   This stage includes females with newly hatched eggs or females who have lost their eggs. Since moulting has not yet taken place, setae will be found on the pleopods.

4) *With head roe (HR).*
   This stage includes females and intersexes with green ovaries visible through the carapace.

5) *Without head roe (UR).*
   This stage includes females and intersexes not fitting into any other category. This stage usually precedes the stage with head roe, but it can also succeed the JH-stage.

Shrimps showing combinations of the above stages are of special importance. For instance, females showing both JH and HR indicate that the females in that sample spawn each year.

AGE DETERMINATION AND GROWTH

Accurate individual age determination of shrimps is not possible, and therefore indirect methods must be used in growth studies.

The present work is based on materials collected during 18 months, and it is therefore not possible to use the deviation method described by SKÚLADÓTTIR (1979). Instead a method has to be used that is based on splitting the observed length distribution of the shrimps in each separate sample into different age-components. There are several such methods in use, all based on the assumption that the length distribution of a year class is normally distributed. The goal is then to estimate the number of normal distributions in an observed length distribution and to estimate the basic statistical parameters (mean, standard deviation and number of individuals) in each of these normal distributions.

Several graphical methods (HARDING 1949, CASSIE 1954, BHATTACHARYA 1967) were evaluated, but they were rejected because the interpretation of the results was considered subjective. For splitting the length distributions into normally distributed components, a method described by TEIGSMARK (in prep.) was used. This method gives estimates of the mean length ($\mu(j,k)$), the standard deviation ($\sigma(j,k)$), and number of individuals ($N(j,k)$) for each separate year class in the sample.

For samples taken with a 35 mm trawl it is necessary to adjust for the selection of the gear, and splitting was then carried out on the adjusted length distributions. For such samples, the actual number of shrimps captured in each year class was then calculated. For samples taken with a fine-meshed trawl splitting was carried out on the unadjusted, observed length distributions.

After splitting the length distribution in the sample, it was decided which year class corresponded to which normal distribution. In this "ordering to year class" process information from the literature (RASMUSSEN 1953) about length-at-age for different populations is of high importance.

PARASITES

The length was measured and sex and reproductive stage determined for each individual parasitized by the bopyride isopode *Phryxus abdominalis* (Krøyer). According to common practice (HORSTED and SMIDT 1956), parasitized individuals were not included in the length distribution of the samples.

HYDROGRAPHY

For each station used to identify the populations, the bottom water temperature was calculated. For stations taken on cruises where hydrographical data were collected, this was calculated from these observations. Hydrographical data from the cruise nearest in time were otherwise used. Temperature estimates for the stations on Cruise 3–78 were derived from measurements collected between 22 June and 13 July 1978, and temperature estimates for the stations on Cruise 3–79 were derived from data collected between 16 June and 12 July 1979.

PART I. IDENTIFICATION OF THE POPULATIONS

METHODS

When examining the samples, information emerges about length-at-age and reproductive characteristics in the form of spawning pattern and age at first spawning as a female. The intention of the analysis is to order the stations from a cruise into groups where the shrimps are homogeneous for the characteristics mentioned above. The method below was used for cruises with many samples, but the analysis was simplified for cruises with only a few samples.

First characteristic: Spawning pattern of the females. This describes either annual or biennial spawning. It can be determined by studying the distribution of the various reproductive stages of females.

Samples from annual spawning populations will contain females who are all in approximately the same reproductive stage. For example, in winter the females will be almost exclusively egg-carriers, and in spring and early summer they will be in the BR+Ø, JH and UR stages.

Samples with biennial spawning will contain females in many different stages in the reproductive cycle. During winter one fraction of the females will be egg-carriers while another fraction will be in the UR stage. During spring and early summer, the fraction carrying eggs during winter will go into the BR+Ø, JH and UR stages, while the fraction not carrying eggs will develop head roe and be ready for spawning.

Spawning pattern was designated "1" or "2" for annual or biennial spawning, respectively. When it was impossible to determine spawning pattern the designation "?" was given. Where spawning pattern is determined, it is accompanied by a subjective indication of the degree of certainty to which the pattern is determined; viz.,

! indicates absolute certainty of determination with no possibility for misinterpretation,

. indicates a small possibility for misinterpretation,

( ) indicates possibility for misinterpretation although one spawning pattern is more probable.

Second characteristic: Age at first spawning as a female.
In each sample the length distribution is split into normally distributed components, and it is then decided which component corresponds to which year class. As the sex-changing year class (intersexes) is known from the sample, the age at first spawning as a female is easily found.

Third characteristic: Length-at-age. In most samples it was possible to identify five or more year classes. The lengths-at-age were compared between the stations on each cruise using the five year classes best represented in the samples. A non-parametric Friedman's test (ZAR 1974) was used to test for equal length-at-age, using the mean length of the five year classes concerned. A matrix of these values was constructed and any missing values calculated as described by SNEDECOR and COCHRAN (1976). Friedman's test was used because the requirements for the parametric two-way analysis of variance were not met.

If the null hypothesis of equal length-at-age on all stations was rejected, a cluster analysis was carried out to place the stations into groups such that the within group variation in length-at-age was less than the variation in the total number of stations. This cluster analysis was based on the euclidian distance between two stations k_1 and k_2 (SNEATH and SOKAL 1973). When using the aforementioned five year classes, this can be expressed as:

$$\Delta(k_1,k_2) = \{\sum_{j=1}^{5} [(\mu(j,k_1) - \mu(j,k_2)]\}^{0.5}$$

When clustering the stations, the UPGMA procedure (SNEATH and SOKAL 1973) was used. The results of this analysis can be visualized by a dendrogram where clusters created at the top include stations with very similar length-at-age. Clusters created lower down indicate increasing differences. By starting at the bottom of the dendrogram and moving upwards, repetitive testing was carried out on the formed clusters until sub-groups of stations with insignificant differences in length-at-age were identified.

RESULTS

CRUISE 1-78

This cruise was carried out in February and March 1978. The sampling localities are shown in Fig. 4.

On station 28 the females spawned every second year, while on stations

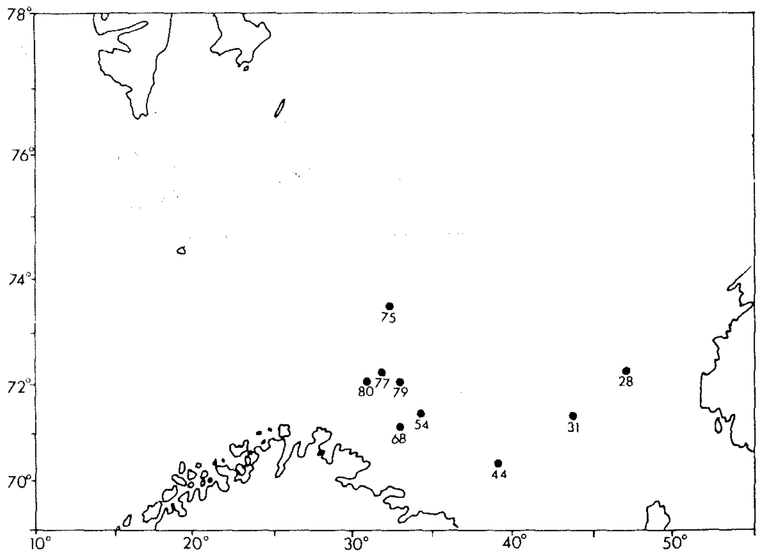

Fig. 4. Sampling localities on Cruise 1–78. Numbers indicate station number.

44–80 they spawned annually (Table 2). Accurate spawning pattern could not be determined on station 31, but the females probably spawned every second year.

The results of splitting the length distributions are given in Table 3. On stations 28 and 31 the 1973 year class changed sex, and on these stations the shrimps therefore spawned for the first time as females 5 years old. On all other stations on this cruise the 1974 year class changed sex, giving the age of first spawning as a female 4 years.

The year classes 1972–1976 were represented in most samples. The missing observation was estimated, and the resulting value is given in Table 3. Length-at-age was significantly different on all stations ($P < 0.001$), and a cluster analysis was therefore carried out. The resulting dendrogram is shown in Fig. 5. On stations 44–80, making out one cluster, length-at-age was not significantly different ($P \approx 0.40$). On stations 28 and 31 however, length-at-age was significantly different ($P \approx 0.025$).

The results from this cruise are summarized in Fig. 6. On stations 44–80 the females spawn for the first time as females 4 years old, and thereafter each year. On these stations length-at-age was not significantly different. On stations 28

Table 2. Spawning pattern at stations on Cruise 1–78.

Station number	28	31	44	54	68	75	77	79	80
Spawning pattern	2!	(2)	1!	1!	1!	1!	1!	1!	1!

Table 3. Results from splitting length distribution of samples from Cruise 1–78. The year class changing sex is underlined. The estimated value is in parenthesis.

Code: 17.50 .95 69 — .95 → $\sigma(j,k)$; 17.50 → $\mu(j,k)$; 69 → $N(j,k)$

Station number	Yearclass 77	76	75	74	73	72	71	70
28		(11.94)	15.25 .95 52	18.30 1.20 139	20.65 .85 139	21.55 .85 148	23.60 .70 64	25.65 .75 23
31		12.40 .70 10	15.60 1.10 102	18.70 .65 41	20.75 .70 36	21.70 .95 76	23.70 .85 70	25.60 .70 25
44		14.25 1.50 100	17.55 .95 252	20.20 .60 103	21.60 .90 132	23.90 .90 8		
54		13.45 .65 18	17.75 1.20 394	20.55 .50 66	21.05 .75 55	23.50 .65 11		
68		13.60 1.00 18	17.75 .90 251	20.20 .95 61	21.30 .95 50	23.50 1.10 13		
75		13.95 1.00 33	17.45 1.00 510	20.10 1.05 250	21.55 .65 165	23.35 .80 111		
77		13.50 .60 28	17.50 .95 359	20.50 .80 116	21.60 .90 84	23.30 .65 79		
79		13.80 .85 3	17.85 .95 78	20.35 .65 107	22.30 .95 130	24.10 1.15 20		
80		13.80 1.00 8	17.80 .95 208	20.20 .95 46	21.85 1.00 66	23.60 1.00 42		

and 31 the shrimps spawn for the first time as females 5 years old, and thereafter every second year. Although length-at-age was significntly different on these two stations, Table 3 shows that the values are very close for all year classes. As the shrimps on these two stations have identical reproductive characteristics they probably are taken from the same unit.

The samples from this cruise therefore seem to be taken from two different units.

CRUISE 3–78

Fig. 7 shows the sampling localities on Cruise 3–78 which was carried out in May and June 1978.

The samples were relatively large, and the spawning pattern could be quite accurately determined in most cases (Table 4). Very few females were found at station 18, and therefore no reliable conclusion can be drawn. At stations 1,2,

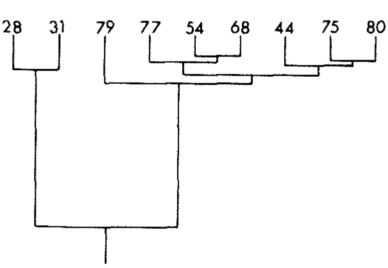

Fig. 5. Dendrogram showing the length-at-age relationship for stations from Cruise 1–78. Numbers indicate station number.

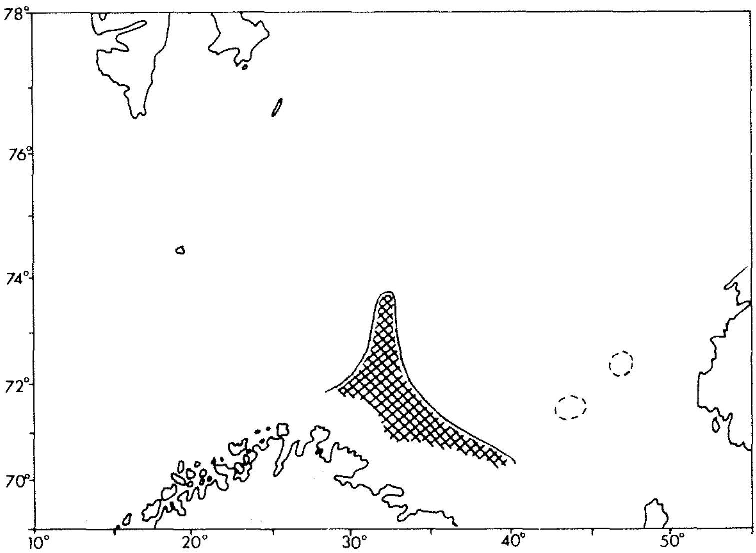

Fig. 6. Summary of the results from Cruise 1–78. Code to be used in this and similar succeeding figures:

Areas with similar growth.

——— Boundary for areas where the shrimps spawned for the first time as females at age 4 years and thereafter annually.

— — — — Boundary for areas where the shrimps spawned for the first time as females at age 5 years and thereafter biennially.

. . . . . . Boundary for areas where the shrimps spawned for the first time as females at age 6 years and thereafter biennially.

and 13–20 annual spawners were found, and at stations 3–12 and 21–25, biennial.

The results of splitting the length distributions are given in Table 5. On stations 1,2, and 13–20 the 1974 year class changed sex, and the shrimps on these stations therefore spawned for the first time as females 4 years old. On stations 21–25 the 1972 year class changed sex, and first spawning as a female therefore takes place at age 6 years. On all other stations, the 1973 year class was changing sex, giving the age at first spawning as a female 5 years.

The year classes 1972–1976 were represented in most samples. The missing observations were estimated, and the resulting values are given in Table 5. As length-at-age was significantly different on all stations ($P < 0.001$), a cluster analysis was carried out. The resulting dendrogram is given in Fig. 8.

Within the cluster including stations 1–3,5,6, and 8–20, length-at-age was

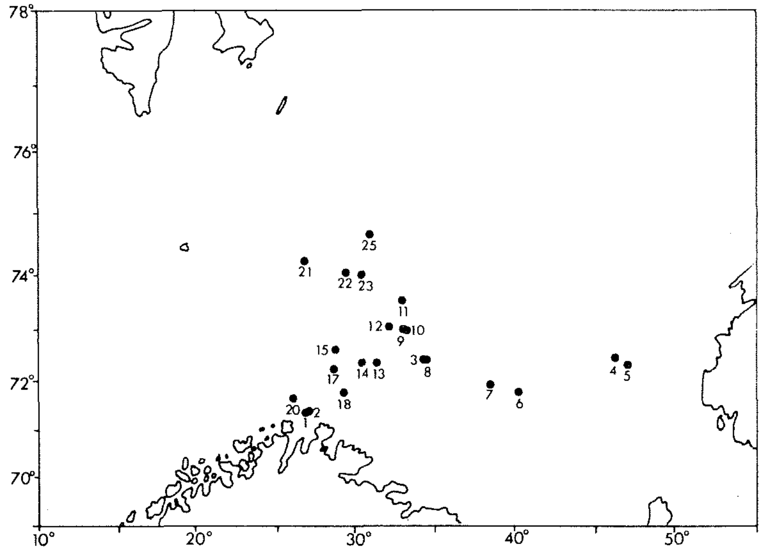

Fig. 7. Sampling localities on Cruise 3—78. Numbers indicate station number.

significantly different (P < 0.001), and this cluster was therefore split into two new clusters. On stations 1,2, and 13–20 the length-at-age was not significantly different (0.10 < P < 0.25), and the same was found for the cluster comprising stations 3,5,6, and 8–12 (0.25 < P < 0.50).

Length-at-age was, however, significantly different on stations 4,7, and 21–25 (0.025 < P < 0.050). Within this cluster, station 4 was most diverging, and it was therefore split off. The resulting cluster composed of stations 7 and 21–25 had identical length-at-age (0.25 < P < 0.50).

On this cruise it was observed that the percentage of intersexes with head roe was a reasonably stable characteristic, and it can give additional information regarding stock structure. Using this characteristic, a clear division was

Table 4. Spawning pattern at stations on Cruise 3–78.

Station number	1	2	3	4	5	6	7	8	9	10	11
Spawning pattern	1!	1!	2!	2!	2!	2!	2.	2!	2!	2!	2!

Station number	12	13	14	15	17	18	20	21	22	23	25
Spawning pattern	2!	(1)	1.	(1)	(1)	?	1!	2!	2!	2!	2!

Table 5. Results from splitting length distribution of samples from Cruise 3–78. The year class changing sex is underlined. The estimated values are in parentheses.

Code: 17.50 .95/69/112 — .95 ← σ(j,k); 69 ← N(j,k)-caught; 112 ← N(j,k)-adjusted for selection; 17.50 ↑ μ(j,k)

Station number	Yearclass 77	76	75	74	73	72	71	70	69
1	10.70 –/1/–	14.90 .75/20/39	17.95 .85/220/286	20.40 1.00/85/93	21.35 1.05/40/41	23.10 .85/62/62			
2		14.80 .80/25/56	18.35 1.00/227/294	20.45 .90/60/56	21.70 1.00/105/114	23.30 .90/26/27			
3		13.35 .55/19/61	16.35 .75/89/140	18.45 .90/142/176	20.65 .65/101/113	20.70 .85/22/20	22.75 .75/39/37		
4		11.80 .65/5/30	14.90 1.15/131/300	18.00 1.00/214/270	20.20 .70/108/114	22.35 .65/32/34	24.55 .55/18/18		
5		14.30 .65/90/238	16.15 .90/110/170	18.30 .90/97/126	20.65 .90/77/80	21.60 1.05/26/27	23.20 .90/20/20		
6		13.40 1.05/73/218	15.80 .85/136/244	18.35 .95/161/202	20.60 .70/65/70	21.30 .65/11/10	23.80 .75/7/7		
7	9.30 .50/6/–	11.85 .55/19/104	14.50 1.30/140/370	17.50 1.20/209/266	20.00 .95/47/50	(20.61)	22.30 .60/13/13		
8		12.75 .80/63/63	16.50 1.15/154/154	18.70 1.05/119/119	20.45 1.05/52/52	21.00 .90/40/40	23.40 .80/9/9		
9		13.60 .75/19/19	16.30 1.05/47/47	18.50 .90/112/112	21.00 .85/164/164	20.70 .70/32/32	23.20 .95/80/80		
10		(13.16)	16.60 .65/42/62	18.90 .90/156/189	21.20 .90/122/130	20.85 .90/21/23	23.20 .90/73/73		
11		12.60 1.25/45/174	16.25 1.20/124/224	19.00 .95/152/172	21.35 .70/62/66	20.80 .90/28/28	23.60 .75/22/22		
12		(13.36)	16.70 .75/61/88	18.75 1.15/104/128	21.30 1.00/109/124	21.60 .95/90/86	23.20 1.00/27/25		
13		13.80 .55/15/40	17.40 1.30/162/234	20.50 1.30/74/78	21.45 .90/123/130	23.65 .90/35/35			
14		14.20 .90/46/116	17.40 1.15/262/368	20.85 .70/38/44	21.20 .85/55/55	23.55 .80/30/30			
15		14.40 .90/39/96	17.80 1.10/250/333	21.00 1.10/72/74	21.60 .95/44/47	23.60 .90/4/4			
17		14.85 .95/35/118	17.55 .75/275/366	19.60 .80/91/108	19.80 .70/6/7	22.30 .75/9/9			
18		13.80 .80/26/68	17.50 1.00/282/380	20.55 1.10/47/56	20.80 1.00/20/21	(22.81)			
20		14.45 .65/12/27	17.90 1.10/263/336	20.55 1.10/83/104	21.00 1.00/53/54	23.20 1.05/45/45			
21		10.80 .50/13/102	14.20 1.20/58/156	17.25 .85/119/160	19.40 .80/126/148	21.30 1.00/88/96	21.50 .70/28/28	23.10 .90/5/5	24.30 .75/12/12
22		11.35 .50/6/53	14.55 .70/51/115	17.10 .90/68/95	19.40 .65/62/74	21.50 .90/120/124	21.30 1.15/52/58	22.95 .80/29/27	25.20 .65/20/20
23	8.15 .35/2	11.65 .75/10/68	14.15 .95/36/91	16.90 .95/75/108	19.25 1.10/126/153	21.30 .80/92/102	21.65 1.00/46/42	22.90 .95/35/35	25.00 .90/23/23
25		(11.81)	14.30 1.00/27/70	17.00 1.00/76/111	19.60 .95/76/81	21.25 .95/116/128	21.45 .70/21/21	23.65 .85/12/10	23.65 .80/34/36

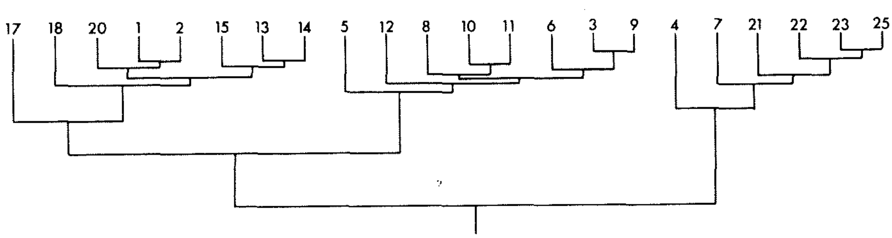

Fig. 8. Dendrogram showing the length-at-age relationship for stations from Cruise 3–78. Numbers indicate station number.

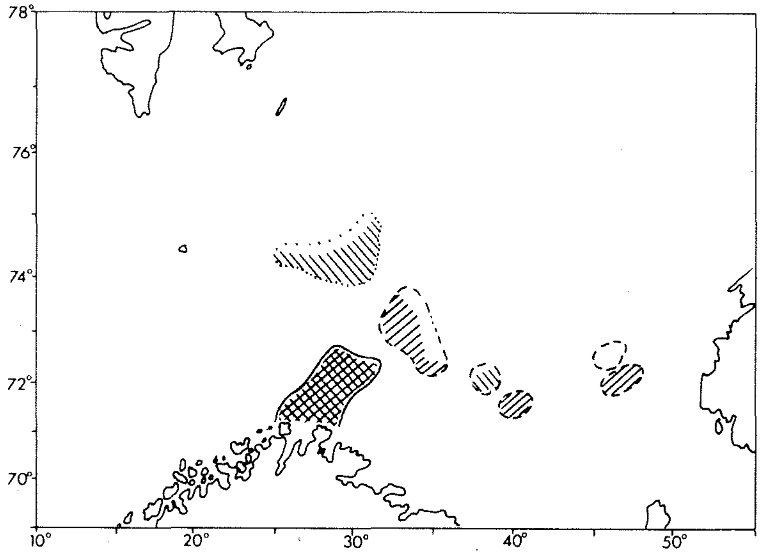

Fig. 9. Summary of the results from Cruise 3–78. Code as in Fig. 6.

observed between stations 1,2, and 13–20 where the females spawn annually (mean: 20%, range: 0% and 61%) and the adjacent stations 3 and 8–12 where the females spawn biennially (mean: 96%, range: 91% and 99%).

The results from this cruise are summarized in Fig. 9. On stations 1,2, and 13–20 the shrimps had first spawning as a female 4 years old and thereafter most probably spawning each year. The shrimps on these stations also had identical length-at-age. On stations 21–25 the shrimps had first spawning as a female 6 years old and thereafter spawning every second year. On these stations length-at-age was identical. On the other stations the females spawned for the first time 5 years old and thereafter every second year. Within this group of stations, length-at-age was identical on stations 3,5,6, and 8–12, while it was diverging on stations 4 and 7. Station 4 could not be linked to any other station on the basis of length-at-age, while station 7 showed high affinity to stations 21–25.

The samples from this cruise therefore seem to be taken from three different units.

CRUISE 1-79

This cruise was carried out from the end of January to the beginning of March 1979. The sampling localities are shown in Fig. 10.

On this cruise the samples were relatively small, and therefore the results are less reliable than those from the other cruises. It was especially difficult to determine spawning pattern at stations 20 and 21 in the eastern part of the Barents Sea (Table 6). For the other stations spawning was found to be annual.

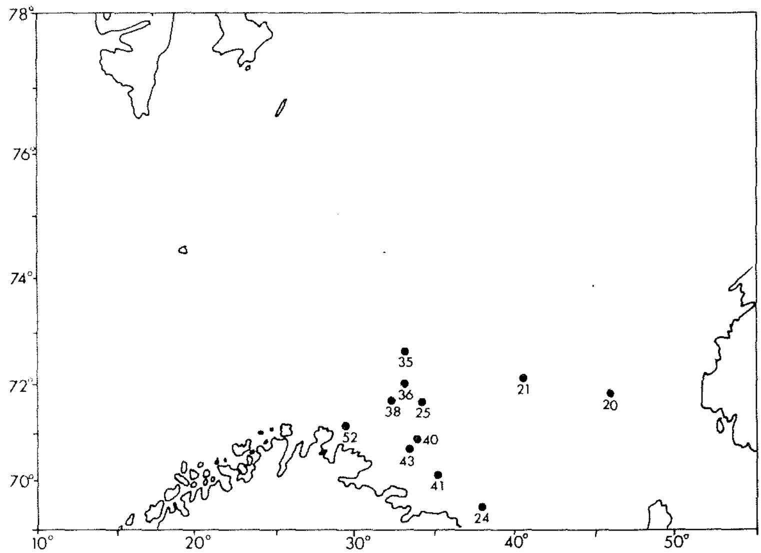

Fig. 10. Sampling localities on Cruise 1–79. Numbers indicate station number.

With the exception of station 35, the results concerning length-at-age and age at sex-change are reliable. Station 35 must, however, be considered separately. Here the youngest captured year class had a mean length of 17.80 mm which could have been assigned equally well to the 1975 or the 1976 year class. It was decided to place these specimens in the 1976 year class because females at this station probably spawn each year.

The results of splitting the length distributions are given on Table 7. On stations 20 and 21 the 1974 year class changed sex, and the shrimps on these stations therefore spawned for the first time as females 5 years old. On all other stations the 1975 year class was changing sex, implying first spawning as a female 4 years old.

The year classes 1973–1977 were found in nearly all samples. The missing observations were estimated, and the resulting values are given in Table 7. On the basis of the observed and estimated mean values of these year classes, length-at-age was significantly different on all stations combined ($P < 0.001$). A cluster analysis was then carried out, and the resulting dendrogram is given in Fig. 11.

Within the cluster including stations 24–52, length-at-age was significantly

Table 6. Spawning pattern at stations on Cruise 1–79.

Station number	20	21	24	25	35	36	38	40	41	43	52
Spawning pattern	(1)	(2)	1.	1.	(1)	1.	1!	1!	1!	1!	1!

Table 7. Results from splitting length distribution of samples from Cruise 1–79. The year class changing sex is underlined. The estimated values are in parentheses. Code as in Table 3.

Station number	Yearclass 78	77	76	75	74	73	72	71
20		(11.64)	15.70 .80 6	18.55 .80 16	20.90 .90 7	21.20 1,00 166	23.40 1,00 53	25.10 .95 16
21	7.90 - 1	10.60 .90 17	14.10 1,25 104	17.20 1,15 204	20.00 .95 94	21.20 1,00 35		
24		13.00 1,05 13	17.60 .65 66	20.60 .70 102	21.20 .90 7	23.35 .90 22		
25		12.50 .85 5	16.90 1,00 87	20.40 1,05 69	20.85 1,00 47	23.00 1,00 18		
35		(13.36)	17.80 1,05 44	20.55 .90 31	21.30 1,15 67	23.55 .95 55	25.80 .85 8	
36		13.05 .75 2	17.40 1,05 33	19.65 .80 77	21.25 1,05 80	22.60 .75 26		
38		12.75 .65 5	17.40 1,00 174	19.55 .95 117	21.25 .65 103	23.50 .75 41		
40		12.90 .95 108	17.25 .85 200	19.95 .75 84	21.40 .95 32	24.30 .90 5		
41		12.75 .95 82	17.40 1,10 141	20.05 .95 126	21.10 .90 21	23.10 1,05 14		
43		13.90 .90 44	17.20 .90 143	20.20 .85 73	20.80 .85 10	23.10 .95 3		
52		14.00 .90 2	17.75 .75 23	20.15 .70 56	22.50 1,00 22	24.50 1,00 7		

different (0.025 < P < 0.050). In this cluster station 52 was most diverging, and it was therefore split off. Within the cluster including stations 24–43, length-at-age was not significantly different (0.05 < P < 0.10). For stations 20 and 21 no significant difference was found in length-at-age (0.025 < P < 0.050).

The results from the analysis are summarized in Fig. 12. On stations 24–52 the shrimps spawned for the first time as females 4 years old and thereafter each year. On these stations growth was to a large extent identical. The samples from these stations must therefore have been taken from the same unit. Within these stations, station 35 is perhaps diverging. On stations 20 and 21 the shrimps spawned for the first time as females 5 years old. In the cluster analysis these two stations were grouped together, but length-at-age turned out to be significantly different. The spawning pattern is relatively uncertain for these stations, but based on the results for age at sex-change, catching locality

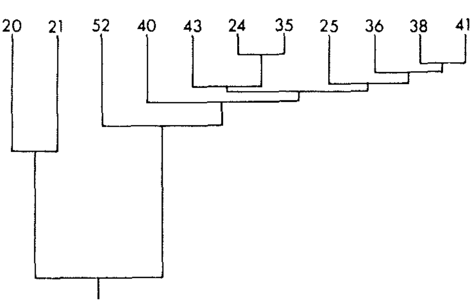

Fig. 11. Dendrogram showing the length-at-age relationship for stations from Cruise 1–79. Numbers indicate station number.

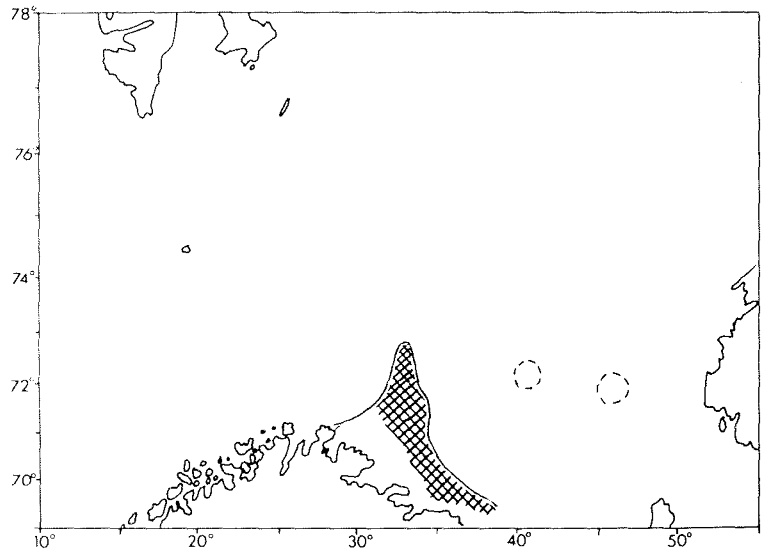

Fig. 12. Summary of the results from Cruise 1–79. Code as in Fig. 6.

and information about length-at-age, it is reasonable to assume spawning every second year on these two stations. It is also reasonable to assume that the samples from these stations are taken from the same unit.

The samples from this cruise therefore seem to be taken from two different units.

CRUISE 3-79

This cruise was carried out in May and June 1979. The sampling localities are shown in Fig. 13.

The spawning pattern of the females on the different stations is given in Table 8. On station 41 it was not possible to determine the spawning pattern. On stations 50–53, certain spawning each year was observed, and on all other stations the females spawned every second year.

The results of splitting the length distributions are given in Table 9. Station

Table 8. Spawning pattern at stations on Cruise 3–79.

Station number	31	35	36	37	38	39	40	41	42	
Spawning pattern	2!	(2)	2!	2!	2!	2.	2!	?	2.	

Station number	43	44	46	47	48	49	50	51	52	53
Spawning pattern	2!	2!	2.	2!	2.	2!	1!	1!	1.	1!

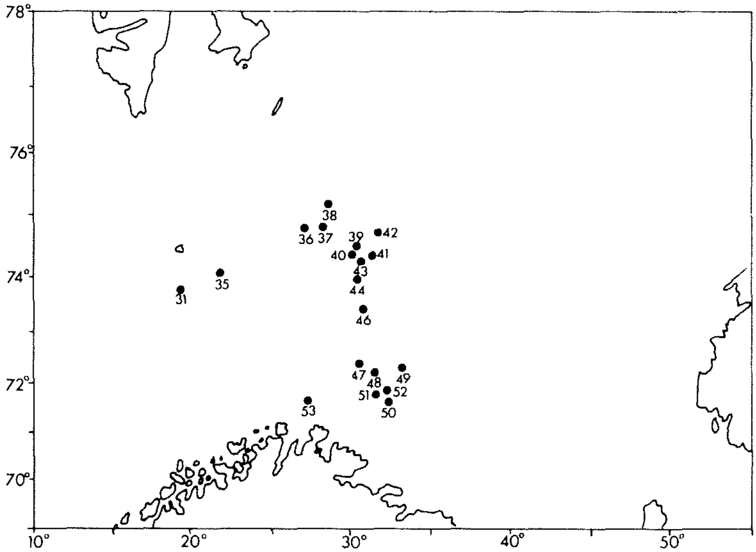

Fig. 13. Sampling localities on Cruise 3–79. Numbers indicate station number.

Table 9. Results from splitting length distribution of samples from Cruise 3–79. The year class changing sex is underlined. The estimated values are in parentheses. Code as in Table 5.

	Yearclass								
Station number	78	77	76	75	74	73	72	71	70
31		10.25 .65/14/165	15.30 1.10/39/80	18.10 1.10/154/195	<u>21.00</u> 1.15/67/75	21.65 1.00/27/29	23.80 .95/44/44		
35		10.35 1.20/34/391	14.70 1.05/162/369	17.60 1.20/206/273	<u>20.85</u> 1.10/30/33	21.85 .85/19/20	23.70 .50/6/6		
36		13.80 .55/17/48	16.30 .95/97/166	18.25 1.05/173/217	<u>21.10</u> .95/95/98	22.10 1.20/16/17	23.90 .80/32/32		
37	9.85 .65/2/32	12.80 .95/10/44	15.90 .85/74/130	18.20 .90/132/171	<u>20.55</u> .70/112/113	22.50 .65/48/52	24.80 .95/19/19		
38	9.75 .95/9/111	13.60 .85/50/157	16.30 1.00/140/235	18.30 .85/135/160	<u>20.80</u> .80/64/69	21.00 .80/23/24	24.10 1.05/14/14		
39		(11.41)	14.10 1.10/29/78	17.15 1.00/69/112	19.00 1.10/174/195	<u>21.45</u> .90/72/73	21.60 .70/32/33	24.60 .95/29/30	
40		11.35 .80/16/102	14.30 1.00/35/92	17.55 1.05/146/196	19.60 .95/115/138	<u>21.70</u> .90/57/68	21.30 1.05/22/23	23.80 1.00/14/14	25.20 .90/15/15
41		(13.09)	16.45 .70/58/92	18.60 .85/143/175	<u>20.80</u> .70/152/166	22.55 .55/51/49	24.65 .75/12/12		
42		(11.73)	(15.02)	17.45 .75/74/102	19.35 .75/110/124	<u>21.15</u> .70/218/233	22.15 .85/53/53	23.60 1.05/41/41	
43		11.20 .65/4/28	14.60 .85/21/54	16.95 .90/99/141	19.25 .80/136/158	<u>21.10</u> 1.00/87/93	21.60 1.00/55/67	23.50 .90/17/13	24.85 .90/33/32
44	11.60 .45/4/27	13.90 .70/13/33	16.20 .80/67/127	18.25 .80/180/213	<u>20.70</u> .70/123/137	22.55 .65/44/45	23.30 .95/18/18		
46	11.75 .55/6/34	(12.78)	16.00 1.00/36/58	18.35 1.25/131/177	<u>21.00</u> 1.05/111/114	21.80 1.05/42/44	23.80 1.00/27/27		
48		13.55 .90/6/21	16.40 .65/49/73	18.65 .80/138/167	<u>20.85</u> 1.00/125/152	22.10 .90/47/33	23.15 1.10/28/31		
49		12.95 .45/10/34	16.20 .85/66/111	18.40 .90/117/147	<u>20.55</u> .80/123/131	20.85 1.00/19/20	23.10 .85/56/56		
50		14.20 .75/54/115	17.85 1.30/281/396	<u>20.25</u> 1.20/92/88	21.40 .85/33/38	23.10 .90/14/14			
51		14.45 .70/18/40	17.80 1.10/176/229	<u>20.80</u> .90/135/166	21.05 .85/41/27	23.40 .95/37/37			
52		13.90 1.15/37/106	17.75 1.35/263/372	<u>19.95</u> 1.25/144/141	20.90 1.15/36/44	23.15 1.05/18/18			
53		15.30 .90/14/14	18.60 1.00/212/212	<u>21.15</u> .75/153/153	21.75 .95/8/8	23.05 .95/63/63			

47 is excluded from this table, because it was not possible to split the length distribution with certainty. On stations 39, 40, 42, and 43 the 1973 year class was changing sex, implying first spawning as a female 6 years old. On stations 50–53 the 1975 year class changed sex, and the shrimps on these stations must therefore spawn for the first time as females 4 years old. On all other stations from this cruise the shrimps had first spawning as a female 5 years old as the 1974 year class was changing sex.

The year classes 1973–1977 were represented on nearly all stations. The missing observations were estimated, and the resulting values are given in Table 9. Length-at-age was significantly different on all stations combined ($P < 0.001$), and a cluster analysis was therefore carried out. Fig. 14 shows the resulting dendrogram.

Stations 50–53, constituting one cluster, had identical length-at-age ($0.05 < P < 0.10$). On stations 31 and 35–49, constituting another cluster, length-at-age was significantly different. This last cluster was therefore split into two new clusters. Within the new cluster formed from stations 36–38, 41 and 44–49, length-at-age was identical ($0.05 < P < 0.10$). Length-at-age was also identical within the new cluster including stations 31, 35, 39, 40, 42, and 43 ($0.10 < P < 0.25$).

It was also noted that the shrimps caught on stations 50–53, where the females spawned annually, had a hard shell and were of first-class quality. On the other stations, where the females spawned every second year, the shrimps were soft-shelled and of very poor quality.

The results from the analysis are summarized in Fig. 15. On stations 50–53, the shrimps spawn for the first time as females 4 years old and thereafter each year. As length-at-age was also identical on these stations, the shrimps must have been taken from the same unit. On stations 39, 40, 42, and 43, the shrimps had first spawning as a female 6 years old and thereafter every second year. Length-at-age was identical on these stations and the shrimps must have been

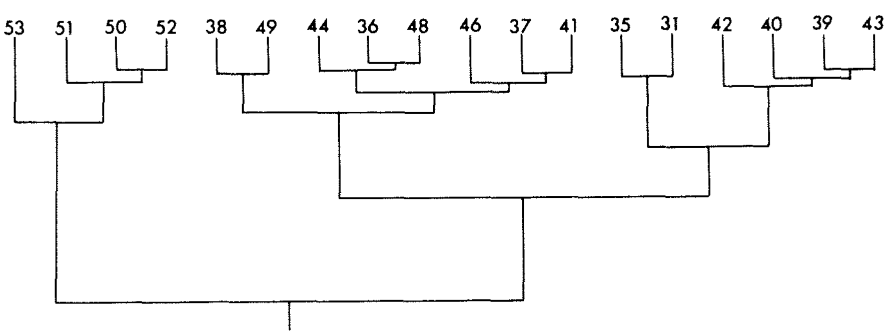

Fig. 14. Dendrogram showing the length-at-age relationship for stations from Cruise 3–79. Numbers indicate station number.

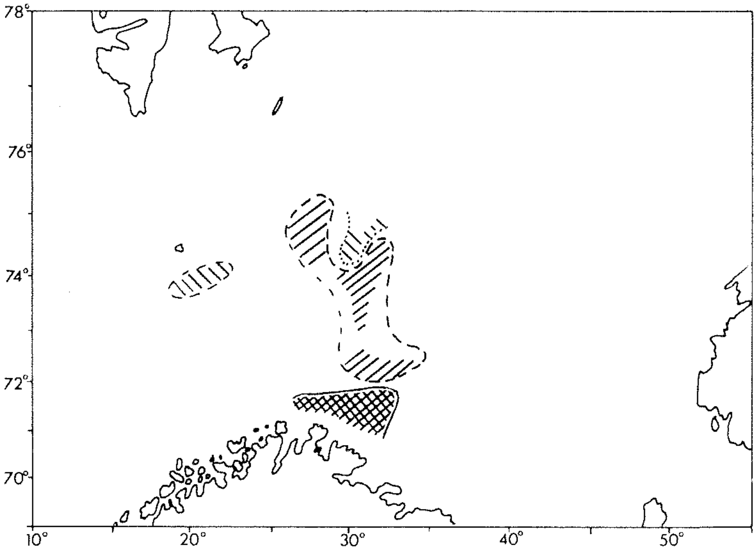

Fig. 15. Summary of the results from Cruise 3–79. Code as in Fig. 6.

taken from the same unit. On the other stations the shrimps spawned for the first time as females 5 years old and thereafter every second year. Within this group of stations, stations 31 and 35 were diverging with respect to length-at-age. On all the other stations length-at-age was identical. For stations 31 and 35 it was difficult to assign the normal distributions to year classes because the year class with a mean length of 10–11 mm could not be aged with certainty. The samples from this cruise therefore seem to be taken from three different units.

CRUISE 2-78

This cruise was carried out in April 1978, and two samples were taken from the western part of the Barents Sea (Fig. 16).

On these stations the females were found to spawn every second year. The results of splitting the length distributions are more uncertain (Table 10). Approximately the same pattern of normal distributions is found in the two

Table 10. Results from splitting length distribution of samples from Cruise 2–78. The year class changing sex is underlined. Code as in Table 3.

	Yearclass					
Station number	76	75	74	73	72	71
111	10.80 .60 28	14.30 .90 22	18.30 1.05 250	20.65 .80 123	22.50 .80 74	24.75 .75 18
116		14.65 .80 4	18.40 1.10 68	20.50 .80 48	22.00 .80 12	24.50 1.00 8

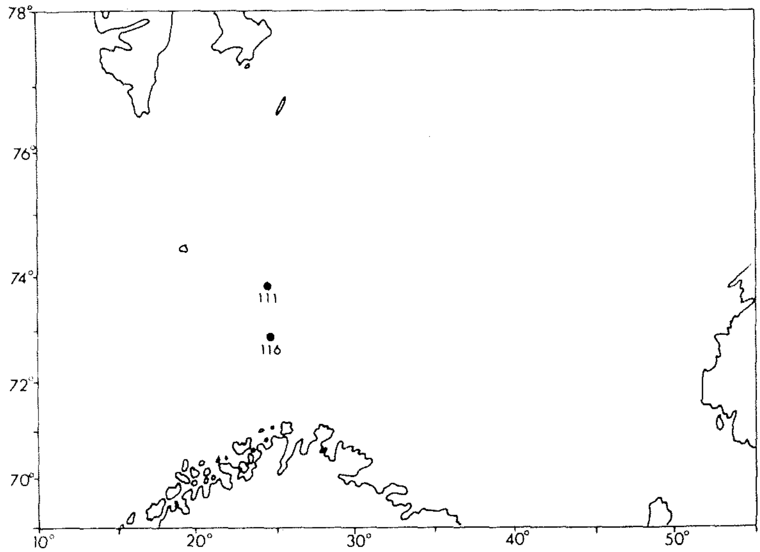

Fig. 16. Sampling localities on Cruise 2–78. Numbers indicate station number.

samples, and they can therefore be treated together. As for stations 31–35 on Cruise 3–79, the ordering by year classes is uncertain because the normal distribution with a mean value of 10–11 mm cannot be aged with certainty. It can correspond to either the 1976 year class or the 1977 year class. As the females on these stations spawn every second year, it is most probably the 1976 year class. If this is accepted, then the shrimps on these stations change sex 5 years old.

Length-at-age was not significantly different ($0.50 < P < 0.75$), tested on the basis of the year classes 1971–1975.

As was concluded for stations 31 and 35 from Cruise 2–79, the results from this cruise must be used with reservation.

CRUISE 4–78

This cruise was carried out in June 1978. The sampling localities for the two stations are shown in Fig. 17.

On station 147, few females were captured, and it was therefore difficult to determine the spawning pattern. In this sample females with eyed eggs (BR+Ø) and females with setae on the pleopods (JH) were found together with females carrying newly spawned eggs (BR–Ø). It is therefore probable that the females spawn every second year on this station. On station 140 the sample contained only one year class of females, all of whom had moulted after egg-hatching. On the basis of this, it is probable that the females spawn each year.

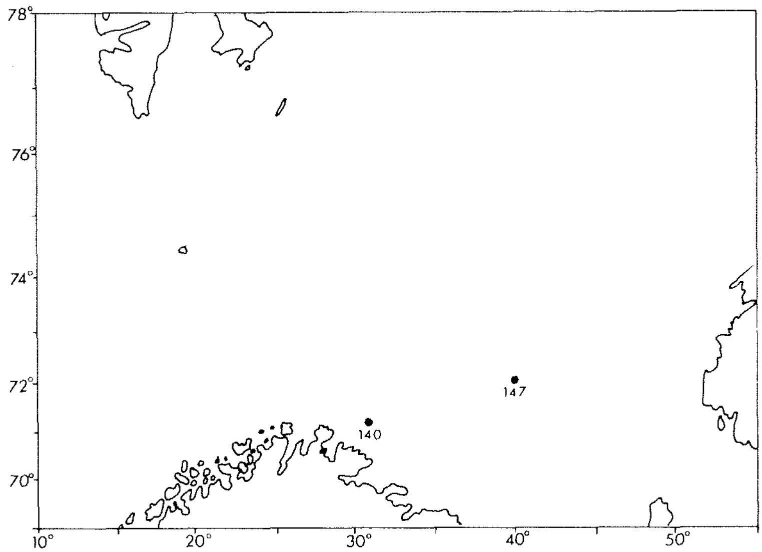

Fig. 17. Sampling localities on Cruise 4–78. Numbers indicate station number.

Table 11 gives the results from the splitting of the length distributions. For both samples the smallest captured year class was assigned to the 1977 year class with certainty. On station 140, sex-change takes place at age 4 years and on station 147 at age 5 years.

Using the year classes 1973-1977 as the basis for the test, length-at-age was found to be significantly different between these stations ($P \approx 0.025$).

The shrimps on these stations have clearly different biological characteristics and the samples therefore seem to be taken from two different units.

CRUISE 5–78

On this cruise one sample was taken in the Tiddly-banken area (Fig. 18) in September 1978.

The female shrimps were found to spawn every second year. The year class hatching eggs during spring and early summer had now moulted, and no setae

Table 11. Results from splitting length distribution of samples from Cruise 4–78. The year class changing sex is underlined. Code as in Table 3.

	Yearclass					
Station number	77	76	75	74	73	72
140	9.75 .70 5	15.00 .90 97	18.05 .80 123	<u>19.55</u> 1.00 96	22.95 1.00 40	
147	9.35 .70 7	13.65 1.45 116	16.30 1.10 128	18.70 1.00 170	<u>20.30</u> 1.10 30	21.20 1.00 20

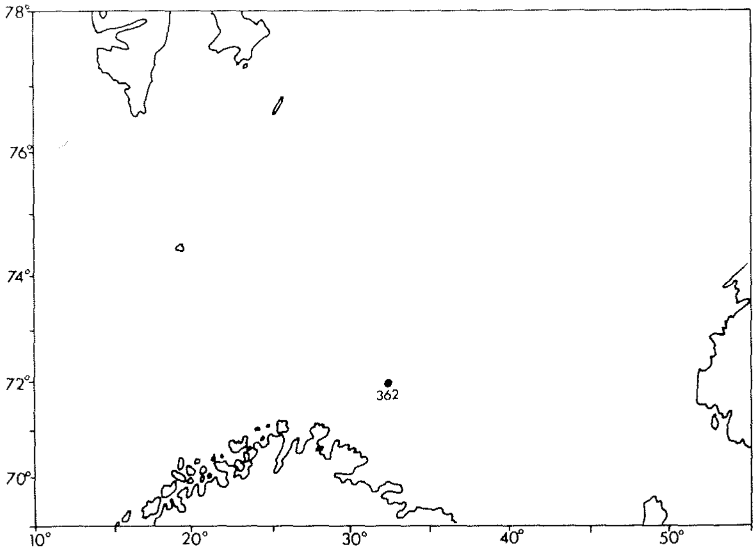

Fig. 18. Sampling localities on Cruise 5–78. Numbers indicate station number.

were found on the pleopods. The results from splitting the length distribution are given in Table 12. In this sample the normal distribution with a mean length of 9.60 mm corresponds to the 1977 year class, and this leads to reliable ordering by year classes. The shrimps first spawn as females 5 years old as the 1973 year class is sex-changing (Table 12).

DISCUSSION

GENERAL PROBLEMS

Growth and reproduction of *P. borealis* has mostly been described for coastal and fjord populations, i.e., populations from small, often isolated, and well-defined areas. The most important fishing areas in the North Atlantic are the offshore grounds at West Greenland and in the Barents Sea. In these areas the possibilities for migrations are larger, and on a given locality it is therefore difficult to ascertain if the same unit of shrimps is found at two different times.

Table 12. Results from splitting length distribution of samples from Cruise 5–78. The year class changing sex is underlined. Code as in Table 3.

	Yearclass						
Station number	77	76	75	74	73	72	71
362	9.60 .75 53	14.20 .90 157	16.80 1.05 92	19.30 .90 58	20.70 .90 48	21.95 .95 34	22.70 1.20 27

To describe the shrimps in these areas, it is therefore necessary to identify and separate possible units, and then follow these units in time.

The life history of *P. borealis* is influenced by several environmental factors, especially by temperature (RASMUSSEN 1953, HORSTED and SMIDT 1956). Within the Barents Sea, differences in bottom water temperature are found, and it can therefore be assumed that the shrimps from different areas will have different biological characteristics. These differences were used here as the basis for the identification of separate units of shrimps.

POSSIBLE CHARACTERISTICS IN THE ANALYSIS

Charcteristics to be used in the identification of these units must be variable within the sampling area, and must also in practical work be usable for all stations. They must also be stable within the sampling period, (i.e., must not change values markedly at a locality during a period of 2–4 weeks), and should also be independent of each other.

The characteristics of length-at-age, spawning pattern and age at sex change were found to fulfill these criteria.

Possible characteristics such as fecundity, variation in year class-strength, length/weight relationship, and hatching and spawning times were rejected on the basis of these criteria.

CONCLUSIONS

Two or three units of *P. borealis* were identified in the materials from the four main cruises.

On the basis of the reproductive characteristics, two units were identified on Cruise 1–78 and again on Cruise 1–79. In the eastern part of the Barents Sea at Gåsbanken and Prestneset, the shrimps spawned for the first time as females 5 years old and thereafter probably every second year. In the southern and central part of the Barents Sea, the shrimps spawned for the first time as females 4 years old, and thereafter annually.

On Cruise 3–78 and on Cruise 3–79, three units were identified on the basis of the reproductive characteristics. In the southernmost part of the Barents Sea at Nordkappleira, the shrimps changed sex at age 4 years and thereafter spawned annually. In the two other units, the females were biennial spawners. West of Sentralbanken, in the northernmost part of the investigated area, the shrimps spawned for the first time as females 6 years old, and on the shrimp grounds at Thor Iversen-banken and Tiddly-banken sex-change took place when the shrimps were 5 years old.

Stations from the four major cruises were also arranged into groups where the shrimps had equal length-at-age, and these groups were in good agreement with the units identified by reproductive characteristics.

With the exception of Cruise 2–78, the results from cruises with only a few samples were in good agreement with the results from the four major cruises.

The results from the analysis based on the three main characteristics, point to the existence of three distinct units of *P. borealis* within the Barents Sea. Use of the additional characteristics of percentage of intersexes with head-roe and hard/soft-shelled shrimps on Cruise 3–78 and Cruise 3–79, also clearly delimits the unit spawning annually.

Based on the analysis it must be concluded that the division into three units of shrimps in the Barents Sea is real. In Part II of this paper it is shown that the identified units are linked to water masses with different temperature, that they have different levels of mortality, and that they have growth parameters that both relatively and absolutely correspond well with the theoretically expected results. This strongly supports the above conclusion. These units are geographically distinct, and they are able to maintain their identity despite opportunities for migration and mixing.

THE POPULATIONS IN THE BARENTS SEA

For the rest of this paper, the identified units will be denoted "populations", and they will be defined on the basis of their reproductive characteristics in the following manner:

(4–1) population: A unit of *P. borealis* in the Barents Sea with first spawning as females 4 years old and thereafter spawning each year.

(5–2) population: A unit of *P. borealis* in the Barents Sea with first spawning as females 5 years old and thereafter spawning every second year.

(6–2) population: A unit of *P. borealis* in the Barents Sea with first spawning as females 6 years old and thereafter spawning every second year.

Each population is here given a designation where the first number refers to age at first spawning as a female and the second, to spawning pattern.

The (4–1) and (6–2) populations are clearly delimited on the basis of their biological characteristics, and they are found in geographically separate parts of the sea (Fig. 19). With the exception of station 52 on Cruise 1–79, length-at-age was similar for each of these two populations for all cruises. With the exception of station 35 on Cruise 1–79 the ordering by year classes was also reliable for these populations.

In the central part of the Barents Sea, the (5–2) population is clearly delimited with reliable ordering by year classes and similar length-at-age on all cruises. Stations taken from the western part of the Barents Sea (Cruise 2–78

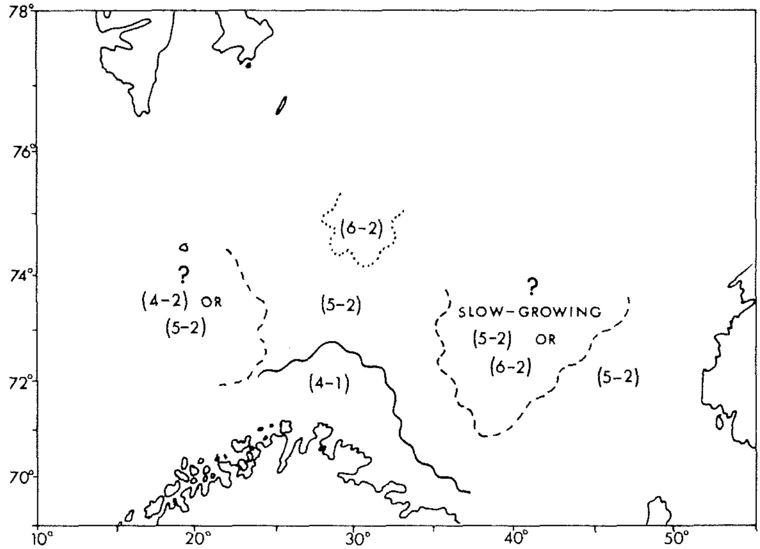

Fig. 19. Probable stock structure of *P. borealis* in the Barents Sea.

and stations 31 and 35 from Cruise 3–79) have also been assigned to the (5–2) population. Data from these stations indicate that the spawning pattern is biennial, but as it was very difficult to assign the normal distributions by year classes, age at sex-change may perhaps be 4 years instead of 5 years. The results from these stations are therefore less clearly defined, and it is possible that these stations should instead have been assigned to a (4–2) population.

In the eastern part of the Barents Sea the results are reliable with regard to the reproductive characteristics. The analysis showed, however, that length-at-age was divergent on some stations. An area of very cold (<0°C) water is found permanently between Tiddlybanken and Gåsbanken. As the shrimps found in cold water grow slower than shrimps found in warm water (see page 416), it is therefore possible that a slow-growing (5–2) population or perhaps a (6–2) population can be found in this area.

The area occupied by each population is to a large extent determined by the hydrographical conditions (see page 421). During 1978 and 1979, the water masses in the Barents Sea were cooled down (Anon. 1979). Under a more normal temperature regime, the populations would probably be found on other localities than those observed in 1978 and 1979. The (4–1) population can be expected to occupy larger areas as the bottom temperature rises again.

The reliability of these conclusions is clearly dependent on the degree of certainty with which the characteristics used in the analysis can be determined.

As accurate splitting of the length distribution in a sample is of vital importance in determining age at sex-change and length-at-age. An accurate splitting demands that the correct number of year classes and the "correct" values for the parameters $\mu(j,k)$, $\sigma(j,k)$, and $N(j,k)$ are found. If the correct number of year classes is found, then the method used for splitting the length distributions will give good estimates for $\mu(j,k)$, $\sigma(j,k)$, and $N(j,k)$.

Published length-at-age data for different shrimp populations were used when assigning the normal distributions to year classes. In cases where many samples had the same pattern of distribution (e.g., Cruise 3–78, st.nos. 21–25), results from the station giving the most reliable results (e.g., st.no. 23) were used to order the distributions from the other stations into the appropriate year classes.

Spawning pattern was evaluated subjectively, but for most stations it could be determined with a high degree of certainty.

Stock structure of *P. borealis* in the Barents Sea has been investigated by USSR scientists. BRYAZGIN (1970) observed that shrimp populations from different parts of the sea had different biological characteristics. As his investigation mainly covered a different part of the sea compared to this investigation, it is difficult to make a direct comparison with his results. BARENBOIM (1978) found statistical significant differences between the length distributions of his samples, and he concluded that this indicated different general populations. The analytical method used by BARENBOIM (1978) has not been adopted in this paper. As differing representations of the separate year classes may cause quite different total length distributions, even when sampling on the same locality, it therefore seems to me that this method, in some situations, may lead to wrong conclusions.

As the three populations observed in the Barents Sea seems able to maintain a distinct identity, little mixing evidently takes place among the bottom-settled shrimps from the different populations. The duration of the pelagic larval period of *P. borealis* must last for many months in the Barents Sea (ALLEN 1959). Shrimp larvae therefore probably drift both between the populations within the Barents Sea and to these populations from those in coastal waters in northern Norway. Due to lower density and a smaller area inhabited by the coastal populations, the production of larvae in coastal waters must be smaller than the total production in the open sea. The influx of larvae from coastal waters is therefore probably of minor importance. Thus the total stock of shrimp in the open Barents Sea may be considered relatively independent of the coastal shrimp populations.

PART II. FURTHER CHARACTERIZATION OF THE POPULATIONS

METHODS

SPAWNING AND HATCHING TIMES

For each station the spawning percentage, i.e. that fraction of the individuals going to spawn that year that actually had completed spawning, was calculated. For each population the mean spawning percentage was then calculated at different times of the year. The hatching percentage, i.e. that fraction of the egg-carrying females that had actually completed hatching, was similarly calculated. Samples from cruises not previously described were used in these calculations, and station data for these samples are given in Table I. For these samples the spawning pattern was determined, but as the length distribution was not split, it was not possible to distinguish between the (5–2) and the (6–2) populations for some stations. Results from such stations are indicated in Tables 13 and 14 by putting them between the lines for these two populations.

FECUNDITY

Samples taken for fecundity studies were frozen. After thawing and measuring the shrimps, the eggs were carefully removed and kept in a 4% formalin solution which was neutralized to prevent precipitation, probably caused by released proteins from the frozen eggs. The eggs were then counted using a binocular lens. The number of eggs was related to carapace length using the power curve $F_{ec} = a'l^{b'}$, where F_{ec} is number of eggs and a′ and b′ are constants.

GROWTH

The constants *a* and *b* in the length-weight relationship $w = al^b$ were estimated by using the regression:

$$\ln w = \ln a + b \ln l$$

The von Bertalanffy growth equation:

$$l_t = L_\infty(1 - e^{-K(t-t_0)})$$

was used to describe growth, and the parameter values in this equation were estimated using a method described by ALLEN (1966). This method gives the best least-squares estimates of the parameters L_∞, K and t_0 and estimates of the variances of these parameters. The theoretical maximum weight W_∞ was estimted for each population by using the L_∞-value in the respective length-weight relationship.

MORTALITY

For each sample, the total mortality (Z) was estimated using the catch curve method (see GULLAND 1969). When adjustments were made for the selectivity of the gear, the corrected values were used. The actual number of each year class in the catch was otherwise used. The mean total mortality was then calculated for the populations observed on each cruise. The mortality estimate of a station was then weighted according to stock density (i.e., catch per nautical mile) on that station.

RESULTS AND DISCUSSION

SPAWNING AND HATCHING TIME

Spawning time

Table 13 gives the mean spawning percentage for each population at different times of the year.

Due to the small amount of materials collected during autumn it is not possible to determine the accurate spawning time for each population. However, the results show that the (4–2) population spawns later in the autumn than the two other populations. The results also indicate that the (6–2) population spawns a little earlier than the (5–2) population, but because of variable single station estimates within a population on a given cruise, it is difficult to conclude anything with certainty concerning the relationship between these two populations. Based on the available information it is proposed that the (5–2) and (6–2) populations spawn from the middle of July to the middle of September and the (4–1) population, from the middle of September to the end of October.

Hatching time

In Table 14 the mean hatching percentage is given for each population at different times of the year. In both years peak hatching occurred in May, and the hatching was nearly completed in June. During spring and early summer 1979, the (4–1) and the (5–2) populations were investigated at two different times. Assuming a normal distribution of hatching in time, then the date of peak (50%) hatching can be estimated by plotting spawning percentage against time on probability paper. The following dates for 50% hatching were then found:

(4–1) population: approximately 1 June
(5–2) population: approximately 15 May

Assuming also that hatching in the (6–2) population has approximately the same time span as the two other populations, 1 May is found as the approximate date of peak hatching for this population. These dates are in

Table 13. Mean spawning percentage of females in the populations at different times during the year. The range of observed values is given in parentheses.

	Date and year							
	1978					1979		
Population	4–17/5	13–14/6	23–26/6	1/9	20–23/10	10–22/5	12–23/6	15/7
(4–1)	0%	–	0%	–	–	0%	1% (0%–3%)	–
(5–2)	0%	–	12%	11%	100%	0%	22% (6%–56%)	95%
(6–2)	–	17% (8%–24%)	–	–		–	32% (8%–49%)	

Table 14. Mean hatching percentage of the populations at different times during the year. The range of observed values is given in parentheses.

	Date and year						
	1978				1979		
Population	20–22/4	4–17/5	13–14/6	23–26/6	10–22/5	12–23/6	15/7
(4–1)	–	54% (5%–96%)	–	100%	16%	89% (81%–100%)	–
(5–2)	0%	62% (35%–87%)	–	60%	61% (23%–85%)	93% (79%–100%)	100%
(6–2)	–	–	97% (96%–100%)	–	–	95% (85%–99%)	

reasonable good agreement with the results to be expected according to RASMUSSEN (1953) who found hatching to take place during March and April in southern Norway and approximately two months later in the Spitsbergen area. It is surprising, however, that the (4–1) population has the later date of hatching of the populations. This may be an artifact of the abnormal temperature regime in the Barents Sea during the time of the investigation.

Summary

The (6–2) population was found in the coldest and the (4–1) population in the warmest water (see page 416). The (4–1) population displayed a markedly shorter egg-bearing period than the two other populations, which is in agreement with previous studies (ALLEN 1959).

Relatively little difference was observed in dates of peak hatching among the three populations. The results show that the (4–1) population spawn markedly later in the autumn than the other two populations. In the Barents Sea, duration of the egg-bearing period therefore seems to be regulated mainly by differences in spawning time. At Iceland, however, hatching time varied more than spawning time (JÓNSSON and HALLGRÍMSSON 1978).

FECUNDITY

Fecundity study samples were taken from the following populations:

St. nr.	Cruise	Population	Sample designation
28	1–78	(5–2)	(5–2)–78
77	1–78	(4–1)	(4–1)–78
20	1–79	(5–2)	(5–2)–79
52	1–79	(4–1)	(4–1)–79
39	3–79	(6–2)	(6–2)–79

The estimated values of the constants a′ and b′ for the different samples are given in Table 15. In Fig. 20, the number of eggs is plotted against carapace length, and the estimated regression curves are also indicated. These curves were significantly different ($P<0.001$). The variation within a population

Table 15. Length/fecundity relationship. The constants in the relationship $F_{ec} = a' l^{b'}$ and coefficient of determination for the different samples.

Sample	a'	b'	r^2	N
(4–1)–78	0.0552	3.16	0.539	56
(5–2)–78	0.0596	3.00	0.354	42
(4–1)–79	0.0228	3.52	0.804	30
(5–2)–79	0.0075	3.77	0.705	47
(6–2)–79	0.0129	3.64	0.691	53

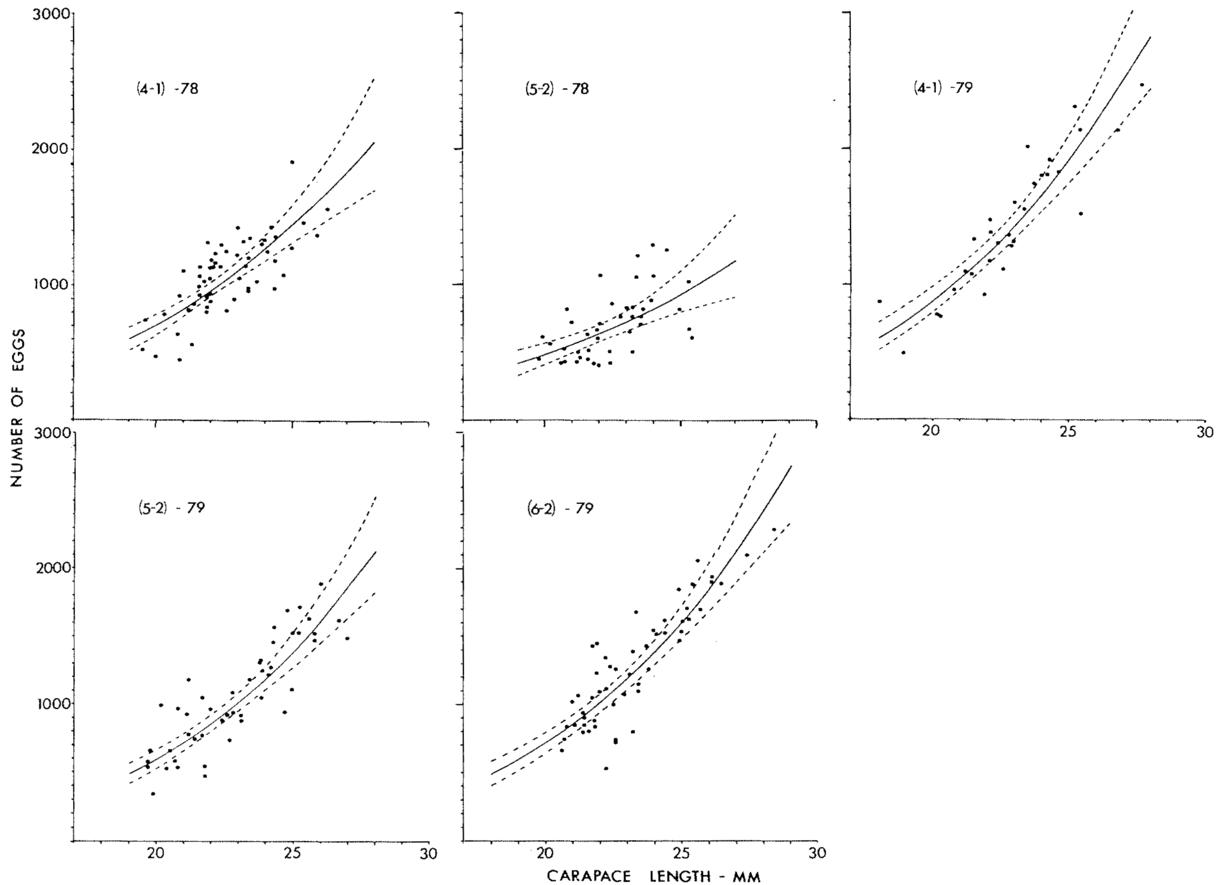

Fig. 20. Number of eggs versus carapace length, the regression curve $F_{ec} = a' l^{b'}$ (__________) and the 95% confidence interval for the regression curve (— — — — —).

during successive years is as great as the variation between the populations in a single year (Fig. 21), making it very difficult to make a conclusive statement about the fecundity of the different populations in the Barents Sea.

The power curve was used to describe the relationship between length and number of eggs even though the linear relationship gave a slightly better fit for most samples. The power curve was used as there is reason to believe that the relationship is *not* linear. THOMASSEN (1977) did, however, use the linear relationship while SKÚLADÓTTIR *et al.* (1978) used the power curve.

In ANON. (1977) it is indicated that the females in northern waters have a higher fecundity than in the North Sea. Fig. 22 gives the relationship between carapace length and fecundity for the extreme observations from the Barents Sea and also for several populations outside this area. The curves for the two southernmost populations (Torungen and Oslofjorden) lie above the curves from the northerly populations while the results for most other populations seem to fit quite well with the results from the Barents Sea. Fecundity therefore seems to be mainly the same, at least in the northeast Atlantic populations.

For both the (4–1) and the (5–2) population a higher fecundity was observed in 1979 than in 1978 (Fig. 21). It is difficult to find a reasonable explanation for

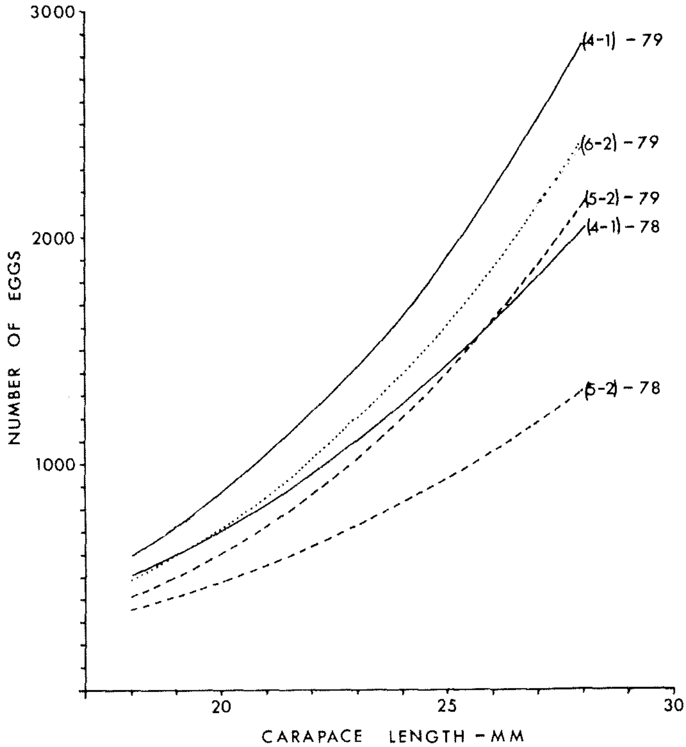

Fig. 21. The regression curves of the five samples.

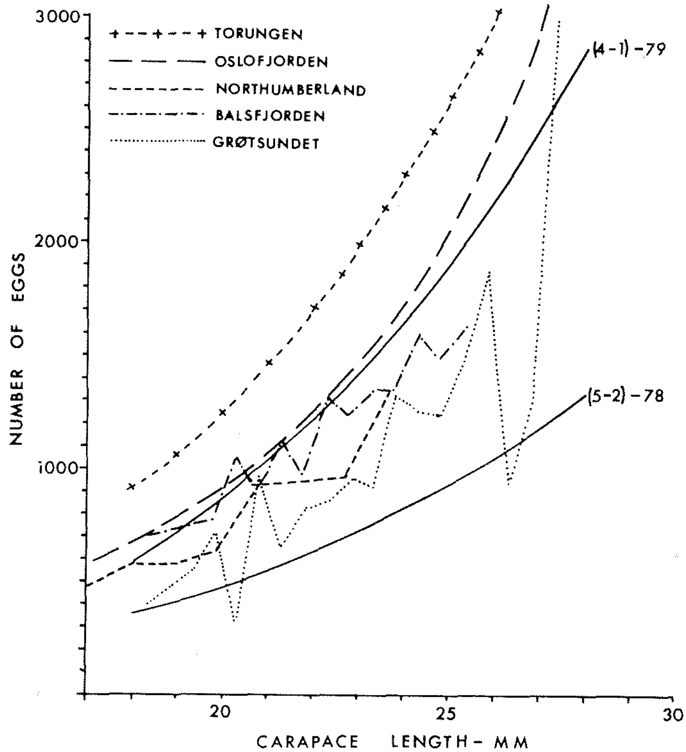

Fig. 22. Length-fecundity relationship for the samples (5–2)–78 and (4–1)–79 from the Barents Sea and for some other populations outside this area. Data for Torungen are taken from Bøhle (1977), for Oslofjorden from Rasmussen (1953), for Northumberland from Allen (1959) and Balsfjorden and Grøtsundet from Thomassen (1977).

this increase in fecundity. Shrimps have, however, small nutritive reserves (Anon. 1968), and it is therefore possible that the available amounts of food during the time prior to spawning can be of importance for the production of eggs. On the fields where the (4–1) population was observed, the density of shrimps was markedly lower during 1978 (Anon. 1979). It is therefore possible that the shrimps that year had better food conditions and thereby the possibility for higher fecundity.

GROWTH

Length-weight relationship

A length-weight relationship was calculated for most samples from the four main cruises. Detailed statistical analyses of the samples were not performed due to difficulties with sample treatment. Table 16 gives the estimated constants in the regression $\ln w = \ln a + b \ln l$ for the populations on the

Table 16. Length/weight relationship. Parameters of the regression line ln W = ln a + b · ln l and coefficient of determination for the populations on different cruises and total values for each population.

Population	Cruise	N	b	95% Conf.lim.	ln a	r^2
(4–1)	Cruise 1–78	152	3.150	± 0.095	− 7.7473	0.966
(4–1)	Cruise 3–78	453	3.161	± 0.047	− 7.7782	0.978
(4–1)	Cruise 1–79	411	3.211	± 0.056	− 7.9150	0.969
(4–1)	Cruise 3–79	207	2.945	± 0.053	− 7.1782	0.983
(5–2)	Cruise 1–78	87	2.992	± 0.101	− 7.2642	0.976
(5–2)	Cruise 3–78	483	3.050	± 0.034	− 7.4639	0.985
(5–2)	Cruise 1–79	108	3.195	± 0.066	− 7.9340	0.989
(5–2)	Cruise 3–79	466	3.111	± 0.037	− 7.6925	0.984
(6–2)	Cruise 3–78	258	3.125	± 0.044	− 7.7344	0.986
(6–2)	Cruise 3–79	206	3.069	± 0.048	− 7.5928	0.987
(4–1)	Pooled	1223	3.150	± 0.029	− 7.7487	0.975
(5–2)	Pooled	1144	3.097	± 0.023	− 7.6398	0.984
(6–2)	Pooled	464	3.103	±0.033	− 7.6792	0.987

different cruises. By pooling all observations from each population, the following length-weight relationships were found:

$$(4\text{–}1)\ \text{population} : w = 4.313 \cdot 10^{-3}\ l^{3.150}$$
$$(5\text{–}2)\ \text{population} : w = 4.809 \cdot 10^{-3}\ l^{3.097}$$
$$(6\text{–}2)\ \text{population} : w = 4.623 \cdot 10^{-3}\ l^{3.103}$$

For the (6–2) population, only samples taken during summer were used, while for the two other populations winter samples were also included. A seasonal variation in condition will influence the length-weight relationship, and the results from the different populations are therefore not directly comparable.

For the populations of *P. borealis* in the North Sea, b was found to be 2.551 for the Fladen stock and 2.618 for the Skagerrak stock whereas for the populations at Iceland b was found to be 3.05 (Anon. 1977). Since the Barents Sea populations were observed to have a b value from 3.10 to 3.15, these probably bear a closer relationship to the Icelandic Populations than to the North Sea populations.

Growth equations

When calculating the growth equations, data from stations where ordering by year classes was uncertain (Cruise 2–78 and stations 31 and 35 from Cruise 3–79), were excluded. Because of a relatively long pelagic phase (Allen 1959), larval drift must take place between the populations. The same date of birth was therefore used for all populations, and it was set as 15 May.

The following growth equations were then obtained:

(4–1) population:

$$L_t = 25.61 \text{ mm } (1 - e^{-0.374(t+0.24)})$$
$$\hat{V}(L_\infty) = 0.05032$$
$$\hat{V}(K) = 0.00018$$
$$\hat{V}(t_0) = 0.00360$$
$$W_\infty = 11.78 \text{ g.}$$

(5–2) population:

$$L_t = 26.70 \text{ mm } (1 - e^{-0.283(t+0.19)})$$
$$\hat{V}(L_\infty) = 0.01898$$
$$\hat{V}(K) = 0.00002$$
$$\hat{V}(t_0) = 0.00079$$
$$W_\infty = 12.59 \text{ g.}$$

(6–2) population:

$$L_t = 27.44 \text{ mm } (1 - e^{-0.235(t+0.10)})$$
$$\hat{V}(L_\infty) = 0.04394$$
$$\hat{V}(K) = 0.00004$$
$$\hat{V}(t_0) = 0.00319$$
$$W_\infty = 13.43 \text{ g.}$$

Fig. 23 shows the observed values of length-at-age and the calculated growth curves, and in Fig. 24 the different growth curves are compared.

In many samples, individuals were found with a length greater than that corresponding to the oldest year class positively identified. Shrimps older than those which could be accurately determined therefore exist. For each population the maximum age, T_{max} (= t_λ) was then set at the nearest year above the highest age observed with certainty. This gives a T_{max} of 7 years for the (4–1) population, 8 years for the (5–2) population and 10 years for the (6–2) population. This method of calculating T_{max} is not very different from that used by CHARNOV (1979).

Shrimp populations with rapid growth have a shorter lifespan than more slow-growing populations (RASMUSSEN 1953, ANON. 1977). CHARNOV (1979) arrived at the following relationship between $1/T_{max}$ and the parameter K in the von Bertalanffy growth equation for pandalid shrimps:

$$K = 2.35/T_{max} \qquad \text{(Eq. 1)}$$

By using this relationship for each population, K-values are found that are in reasonable proximity to the K-values calculated earlier.

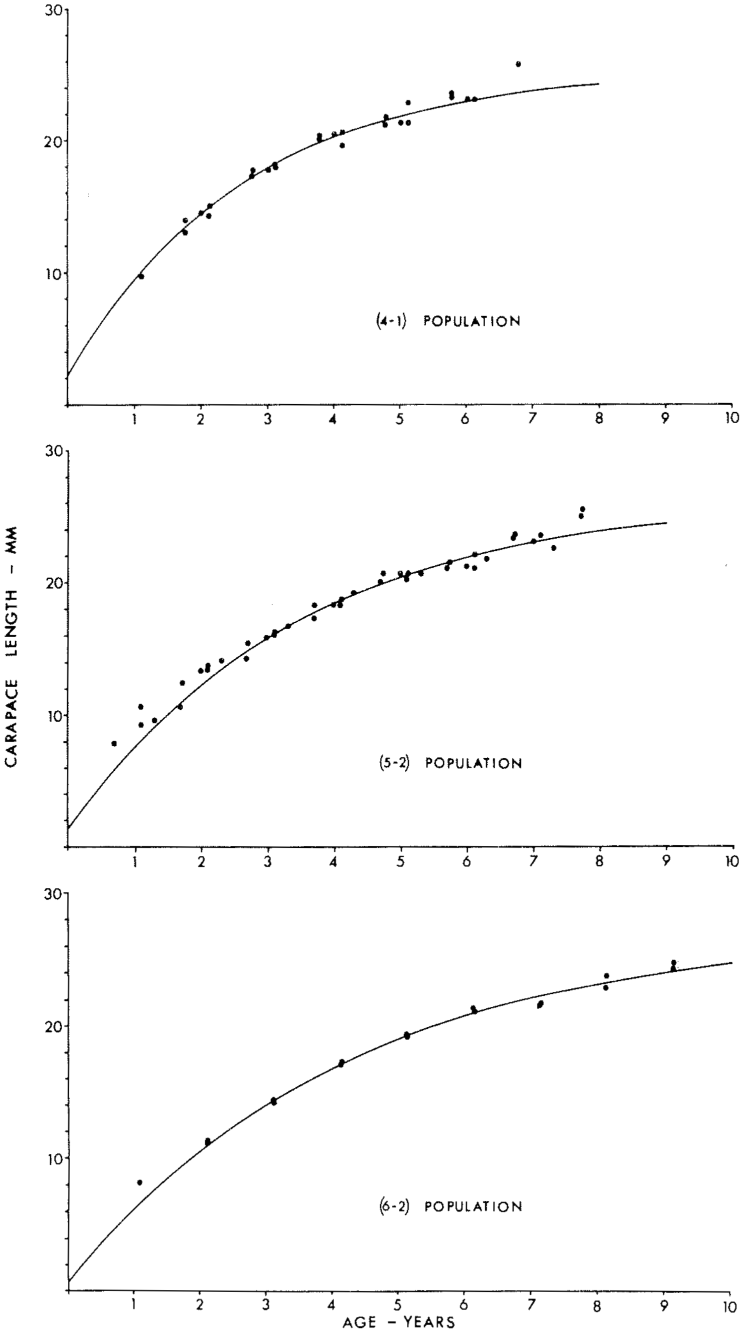

Fig. 23. Observed values for length-at-age and calculated growth curves for the populations.

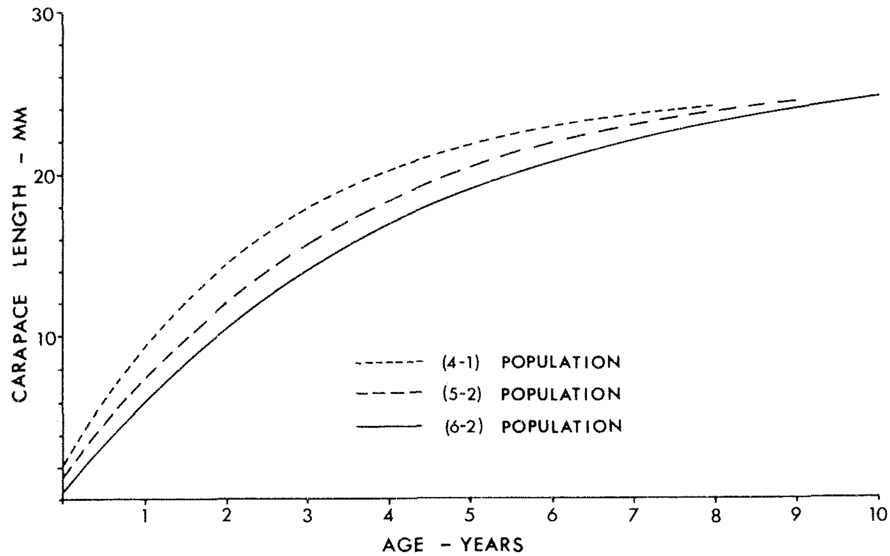

Fig. 24. Growth curves for the three populations.

Fig. 25 shows the temperature range where the populations were observed on each cruise. The (4–1) population was found in water masses with a mean temperature of approximately 2°C. Most observations were in the interval 1–3°C. The (5–2) population was found in several parts of the Barents Sea. In the eastern part of the sea, the bottom water was abnormally cold during the time of the investigation, and it is uncertain whether the samples taken from the western part of the sea belonged to the (5–2) population. Therefore only the temperature observations from the central part of the Barents Sea are considered representative for the water masses where the (5–2) population lives under normal conditions. The mean temperature of the water where this population was found, was slightly below 1°C, and the maximum temperature was 1.5°C. In most instances the (6–2) population was found in water masses with a temperature slightly above 0°C, and the maximum temperature was 0.7°C.

The (4–1) population with the highest K-value and the lowest L_∞-value is found in the warmest water, and the (6–2) population with the lowest K-value and the highest L_∞-value in the coldest water. This is in agreement with Beverton and Holt (1959) if temperature is assumed to be the most important factor regulating growth. Similar results showing fast growth in warm water and slow growth in cold water, are well known for *P. borealis* (Rasmussen 1953, Horsted and Smidt 1956). It must, however, be noted that temperature is probably only one of several factors of importance in the regulation of growth.

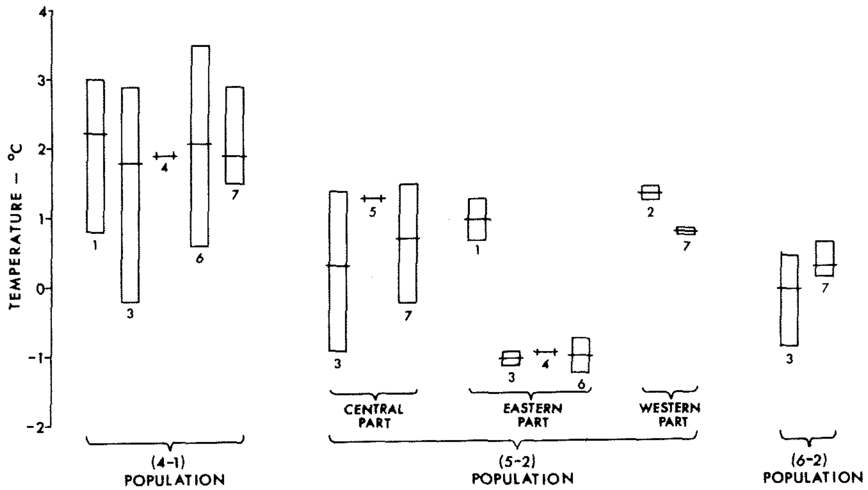

Fig. 25. Temperature range where the populations were observed. Average temperature is marked by a cross-bar. 1 = Cruise 1–78, 2 = Cruise 2–78, 3 = Cruise 3–78, 4 = Cruise 4–78, 5 = Cruise 5–78, 6 = Cruise 1–79 and 7 = Cruise 3–79.

Age at sex-change

RASMUSSEN (1953) showed that most shrimps in southern Norway change sex at the age of 2.5 years. He also showed that the age at sex-change generally increases as one goes northwards along the Norwegian coast, such that the shrimps at Spitsbergen spawn for the first time as females 5 years old. SKÚLADÓTTIR *et al.* (1978) found that the age at sex-change varied among the Icelandic populations, and HORSTED and SMIDT (1956) found populations at West Greenland changing sex at ages of 4 and 5 years.

Thus, the (4–1) and (5–2) populations changing sex 4 and 5 years old respectively correspond to the populations in West-Greenland and Spitsbergen waters. The (6–2) population changes sex at a higher age than has until now been observed.

In my material a tendency towards higher length at sex-change for the most slow-growing populations is observed. At East-Greenland, sex-changing shrimps have been found that are 5–6 mm longer than what is observed in the Barents Sea (TORHEIM, pers. commn.). This is not in agreement with RASMUSSEN (1953) who assumed that sex-change took place at a different age, but at equal length.

The sex-change process seems to last one year for the Barents Sea populations as the length distribution of the intersexes was clearly unimodal. This is not in accordance with BARENBOIM (1978) who found this process to last two years in the northwestern part of the sea.

Table 17. Calculated mean total mortality and range per population and cruise.

Population and cruise	$\bar{Z}$	Range	N
(4–1) population			
Cruise 1–78	0.619	(0.389–1.090)	7
Cruise 3–78	0.825	(0.519–1.448)	8
Cruise 4–78	0.562	–	1
Cruise 1–79	0.925	(0.446–1.358)	9
Cruise 3–79	0.979	(0.664–1.090)	4
(5–2) population			
Central section			
Cruise 3–78	0.609	(0.264–0.720)	6
Cruise 5–78	0.342	–	1
Cruise 3–79	0.737	(0.469–0.926)	8
Eastern section			
Cruise 1–78	0.726	(0.134–0.930)	2
Cruise 3–78	0.818	(0.524–1.172)	4
Cruise 4–78	1.070	–	1
Cruise 1–79	1.154	(0.881–1.187)	2
Western section			
Cruise 2–78	0.811	(0.781–0.840)	2
Cruise 3–79	0.790	(0.542–1.085)	2
(6–2) population			
Cruise 3–78	0.457	(0.331–0.696)	4
Cruise 3–79	0.610	(0.435–0.869)	4

In my samples, no primary females were observed, corresponding to results from other slow-growing populations (CHARNOV 1979).

In this work I have not investigated the age at which the shrimps first function as males. Based on results from other investigations (RASMUSSEN 1953, HORSTED and SMIDT 1956), it is probable that an individual functions as a male for two spawnings before changing sex.

MORTALITY

Table 17 gives the mean mortality for each population on the various cruises. Considerable variation was observed in the single station mortality estimates from a population on an individual cruise. For each population it was, therefore, decided to exclude results from cruises with only one or two samples. For the (5–2) population only results from the central part of the Barents Sea were used, as they were considered most representative of this population. The following total mortality estimates were then obtained:

	Population		
	(4–1)	(5–2)	(6–2)
Cruise 1–78	0.619	–	–
Cruise 3–78	0.825	0.609	0.457
Cruise 1–79	0.925	–	–
Cruise 3–79	0.979	0.737	0.610

For the two cruises where all three populations were sampled, the highest total mortality was observed for the fast-growing (4–1) population and the lowest, for the slow-growing (6–2). A relationship therefore has been observed between a high K-value and a high Z-value. By using Eq. 1 and assuming $Z = 6.4/T_{max}$, CHARNOV (1979) found the following relationship for pandalid shrimps:

$$Z = 2.7 \cdot K$$

By using this relationship and the calculated K-values, the following Z-values were found:

(6–2) population: 0.635
(5–2) population: 0.764
(4–1) population: 1.010

These Z-values are reasonable close to the previously estimated Z-values. It must be noted, however, that it seems a little doubtful to postulate a relationship between Z and K, as the total observed mortality, to a large extent, will depend on the experienced fishing mortality.

For the deep-sea shrimp, natural mortality is caused mainly by fish predators, and especially by cod (ANON. 1977). Based on stomach content investigations (HYLEN *et al.* 1972), cod can be identified as the main predator also in the Barents Sea area. As cod is found mainly in water warmer than 1°C (HARDEN JONES 1968), the (6–2) population should suffer the lowest and the (4–1) population the highest predation-caused natural mortality. It must be noted, however, that for populations living in very cold water, arctic fish species such as *Lycodes spp.* may act as predators (HORSTED and SMIDT 1956). Environmental stress can also cause mortality in these cold-water populations (HORSTED and SMIDT 1956). A relationship between high growth rate and high natural mortality has been observed for many fishes (BEVERTON and HOLT 1959). Such a relationship probably also holds for the shrimp populations in the Barents Sea, giving the highest natural mortality for the fast-growing (4–1) population and the lowest for the slow-growing (6–2).

In the early 1970's the Nordkappleira field was nearly fished out and was then almost totally ignored until 1977 when a limited catch (612 tonnes) was taken (ANON. 1979). If it is assumed that all catches from this field are taken from the (4–1) population, and that this population is not included in any part of the catches from the other shrimp fields, then the total mortality observed for the (4–1) population on Cruise 1–78 should approximately equal natural mortality. This indicates a natural mortality of approximately 0.60 for the (4–1) population. Since natural mortality rates are assumed to be lower in the two other populations, 0.30 was assigned as the most probable value of M for the (6–2) population and 0.40 for the (5–2).

Few natural mortality estimates have been published for *P. borealis*. For the Arnarfjördur population at Iceland, values of 0.20–0.30 are indicated (ANON. 1977), and for the populations at the southwest coast of Iceland where the cod concentrations are higher, 0.50 is proposed. For the populations in the North Sea, natural mortality is assumed to be in the interval 0.50–1.00. The natural mortality rates for the Barents Sea populations are therefore more comparable to those for the Icelandic populations than to those for the North Sea populations.

I have not been able to determine if the assumptions hold for using the catch-curve method, hence the stated mortality estimates should be regarded as approximate values only. It is therefore not possible to say with certainty if the observed increase in total mortality for all three populations from 1978 to 1979 is real. However, an increased fishing pressure, at least for the (4–1) population (ANON. 1979), and the concentration of cod in the western part of the Barents Sea (ANON. 1979) probably causing an increase in natural mortality for both the (4–1) and (5–2) populations, indicate that a real increase in total mortality may have taken place.

For some populations a very high natural mortality has been reported for the females after hatching the eggs or in connection with the second spawning (ALLEN 1959). This has not been observed in my material, and the same natural mortality is therefore assumed for the females, intersexes and males.

MIGRATIONS

Vertical migrations

Eight shrimp samples were collected by pelagic trawl during winter and autumn 1978. Two of these samples were collected more than 300 m above the seabed whereas most other hauls were taken about 200 m above the bottom. This shows that the shrimps can migrate vertically far above the bottom. As all the samples were taken during a period of darkness, and no shrimps were captured pelagically in daylight on these cruises, this migration is probably a response to different light levels.

Males were dominant in these samples (83–100%), and the mean length of the shrimps in the samples was therefore low (12.5–17.8 mm). Samples collected by bottom trawl nearly always yielded a much higher proportion of females and intersexes, and the mean length of the shrimps in these bottom hauls was usually between 19 mm and 20 mm. Even though all size groups take part in this vertical migration, the small males migrate vertically to a larger extent than do the intersexes and females. This is in agreement with BARR (1970).

Horizontal migrations

The material includes one example of a relatively fast and significant change in the distribution area of the (4–1) population. During winter 1978, this population was found far north. The borderline indicated in Fig. 26 includes the area where this population was observed with certainty. As no sampling was conducted at higher latitudes, the real boundaries of distribution may have been even further north.

During summer 1978, the (4–1) population had a much more southerly and westerly distribution (Fig. 26). The (5–2) population was now found in the northernmost part of the area where the (4–1) population was found during winter. This clearly defines the borderline for the area occupied during summer by the (4–1) population. During the period from January to July 1978 a very marked cooling of the bottom water occurred in the Barents Sea, with cold water masses moving westward during spring and early summer (Fig. 27).

It has been shown (page 416) that the three populations are linked to water masses of different temperatures. The movement of cold water westward then probably caused withdrawal of the (4–1) population. The (5–2) population

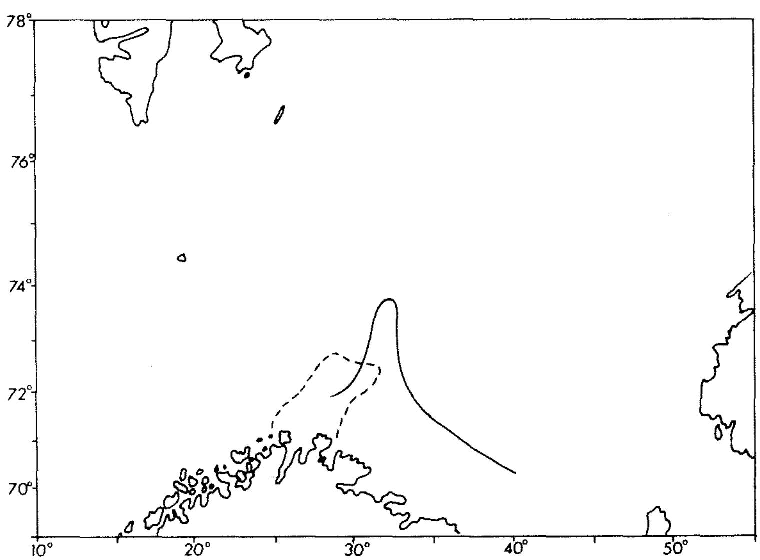

Fig. 26. Areas where the (4–1) population was observed during winter 1978 (————) and summer 1978 (— — — — —).

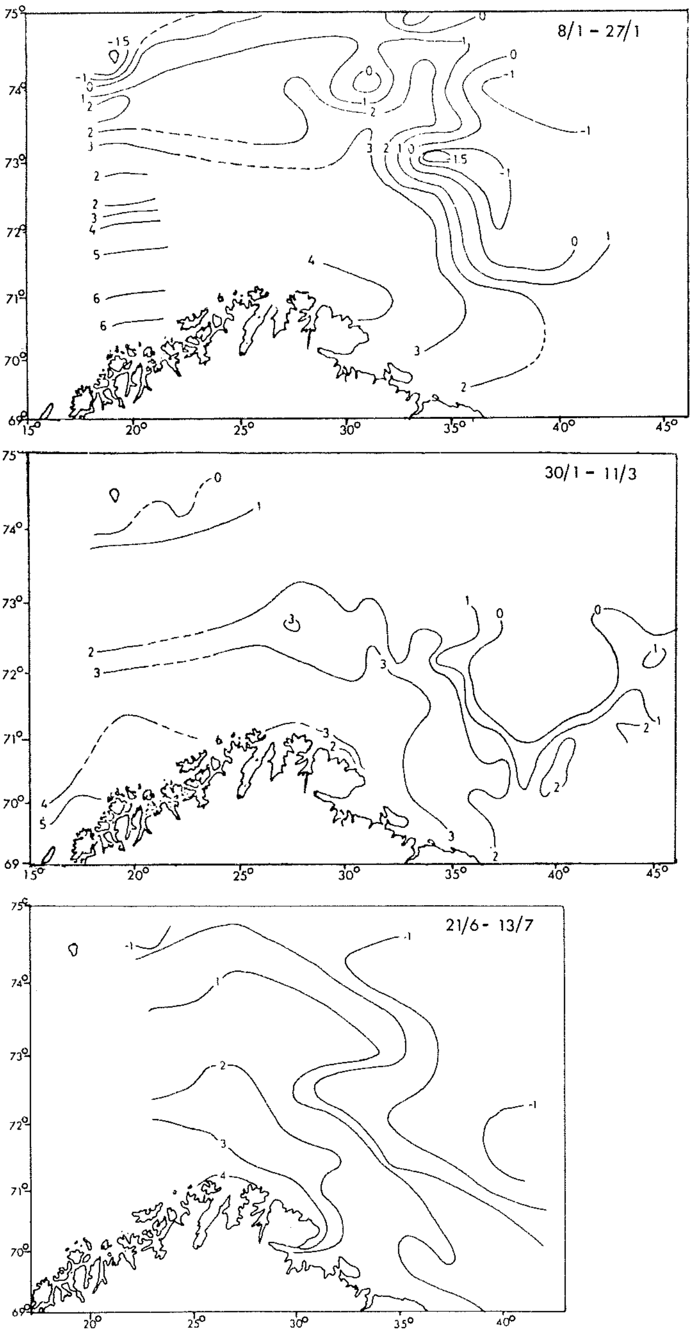

Fig. 27. Bottom water temperature in the Barents Sea during three periods in 1978.

then followed the cold water masses and replaced the (4–1) population in some part of the area. Similar migrations due to changes in the hydrographical conditions have been described by Horsted and Smidt (1956), Rasmussen (1967), and Skúladóttir *et al.* (1978).

PARASITISM

The degree of parasitic infection by *Phryxus abdominalis* was investigated for all samples from cruises used to identify populations. It was hypothesized that this characteristic could vary geographically and therefore be useful in identification of the populations.

However, no significant difference in the degree of infection was found among samples from any cruise. There was also no significant difference between the populations for the two cruises where all three populations were sampled (Cruise 3–78, $0.10<P<0.25$, Cruise 3–79, $0.50<P<0.75$), nor between the different cruises ($0.05<P<0.10$).

The observed degree of infection is low with a grand mean of 0.23% with single-sample values ranging from 0.0% to 1.4%. These values seem to be typical: In Greenland waters usually less than 2% and rarely more than 4% of the individuals were infected (Horsted and Smidt 1956), and at Northumberland there was no observed infection (Allen 1959).

Horsted and Smidt (1956) found that only males were attacked and concluded that the parasite arrested reproductive development in the male stage, and that sex change thus could not take place. My material of infected individuals also consists mostly of males, but some individuals that, according to size, should be males, had their endopodite transformed into the form of an intersex. This was also observed by Rasmussen (1953). This parasite can lead, consequently, to changes in the sexual characteristics of *P. borealis*. This phenomenon has also been observed for other hosts infected by bopyride isopods (Stephensen 1948). One intersex with head roe, but no infected females, was found in the materials on which the present work is based. However, in 1980 and 1981 I found infected egg-carrying females both in Spitsbergen waters and in the open Barents Sea.

The effect of the parasite on the weight of the host was also investigated. The infected individuals were measured for length and weight without the parasite. As a length-weight relationship is known for the non-parasitized individuals for each station used in this test, the weight of a parasitized and a non-parasitized individual of equal length can be compared. Using a Wilcoxon pair-test, no significant difference in weight was found ($0.20<P<0.50$).

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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. biol. Ass. U.K., 38*: 189–220.

ALLEN, K. R. 1966. A method of fitting growth curves of the von Bertalanffy type to observed data. *J. Fish. Res. Bd Can., 23*: 163–179.

ANON. 1968. Proceedings of the world scientific conference on the biology and culture of shrimps and prawns. *FAO Fisheries Reports No. 57, Vol. 1*: 1–75.

ANON. 1972. Report of the first meeting of the ICES Working Group on *Pandalus borealis*. *Coun. Meet. int. Coun. Explor. Sea, 1972* (K:6): 1–5. 3 Tabs, 4 Figs. [Mimeo.]

ANON. 1977. Report of the working group on assessment of *Pandalus borealis* stocks. *Coun. Meet. int. Coun. Explor. Sea, 1977* (K:10): 1–12. 12 Tabs, 8 Figs. [Mimeo.]

ANON. 1979. Ressursoversikt for 1979. *Fisken Hav., 1979* (Særnr. 1): 1–119.

BARENBOIM, B. I. 1978. Populational differences in the prawn *Pandalus borealis* in the Barents Sea. *Hydrobiol. J., 14*(1): 36–39.

BARR, L. 1970. Diel vertical migration of *Pandalus borealis* in Kachemak Bay, Alaska. *J. Fish. Res. Bd Can., 27*: 669–676.

BEVERTON, R. J. H. and HOLT, S. J. 1959. A review of the lifespans and mortality rates of fish in nature, and their relation to growth and other physiological characteristics. P. 142–177 in WOLSTENHOLME, G. E. W. and O'CONNOR, M. ed. *Ciba Foundation. Colloquia on Ageing. Vol. 5. The Lifespan of Animals*. J. and A. Churchill LTD., London.

BHATTACHARYA, C. G. 1967. A simple method of resolution of a distribution into Gaussian components. *Biometrics, 23*: 115–135.

BRYAZGIN, V. F. 1970. On distribution and biology of the shrimp *Pandalus borealis* (Kr.) in the open parts of the Barents Sea. *Mater. Ryb. Issled. Sever. bass., 16*: 93–107. (In Russian).

BRYAZGIN, V. F. 1973. Investigations on ecology and biology of *Pandalus borealis* in open parts of the Northeast Atlantic. *Coun. Meet. int. Coun. Explor. Sea, 1973* (K:29): 1p. 2 Tabs, 2 Figs. [Mimeo.]

BØHLE, B. 1977. Vekst og utvikling av larver og postlarver av dypvannsreke (*Pandalus borealis* KRØYER) ved eksperimentelle forhold. *Fisken og Havet Ser. B, 1977* (10): 1–32.

CASSIE, R. M. 1954. Some uses of probability paper in the analysis of size frequency distributions. *Aust. J. mar. Freshwat. Res., 5*(3): 513–522.

CHARNOV, E. L. 1979.Natural selection and sex change in pandalid shrimp: Test of a life history theory. *Am. Nat., 113*: 715–734.

GULLAND, J. A. 1969. Manual of methods for fish stock assessment. Part 1. Fish population analysis. *FAO Manuals in Fisheries Science, 4*: 1–154.

HARDEN JONES, F. R. 1968. *Fish migration*. Edward Arnold Ltd., London. 325 pp.

HARDING, J. P. 1949. The use of probability paper for the graphical analysis of polymodal frequency distributions. *J. mar. biol. Ass. U.K., 28*: 141–153.

HORSTED, S. A. and SMIDT, E. 1956. The deep sea prawn. (*Pandalus borealis* Kr.) in Greenland waters. *Meddr Danm. Fisk.- og Havunders., 1*(11): 1–118.

HYLEN, A., JAKOBSEN, T., LAHN-JOHANNESSEN, J., SMEDSTAD, O. M. and SÆTRE, R. 1972. Bunnfiskundersøkelser ved Bjørnøya, Spitsbergen og i Barentshavet med F/F «G. O. Sars» 3–20 november 1970. *Fisken Hav., 1972* (1): 25–38.

PALENICHKO, Z. G. 1941. The distribution and life history of the shrimp *Pandalus borealis* Kr. in the Barents Sea. *Zool. Zh., 20*: 398–414. (In Russian).

RASMUSSEN, B. 1953. On the geographical variation in growth and sexual development of the deep sea prawn (*Pandalus borealis* Kr.). *FiskDir. Skr. Ser. HavUnders., 10* (3): 1–160.

RASMUSSEN, B. 1967. Temperaturforhold og rekefiske i Skagerrak 1962–1966. *Fiskets Gang, 47*: 842–847.

RASMUSSEN, B. and ØYNES. P. 1970. Forsøksfiske etter reker i Barentshavet i mars–april 1970. *Fiskets Gang, 56*:587–593.

SKÚLADÓTTIR, U. 1979. Comparing several methods of assessing the maximum sustaintable yield of *Pandalus borealis* in Arnarfjördur. *Rapp. P.-v. Réun. Cons. int. Explor. Mer, 175*: 240–252.

SKÚLADÓTTIR, U., JÓNSSON, E. and HALLGRÍMSSON, I. 1978. Testing for heterogeneity of *Pandalus borealis* populations at Iceland. *Coun. Meet. int. Coun. Explor. Sea, 1978* (K:27): 1–9. 23 Tabs, 20 Figs. [Mimeo.]

SNEATH, P. H. A. and SOKAL, R. R. 1973. *Numerical taxonomy*. W. H. Freeman and Company, San Francisco. 573 pp.

SNEDECOR, G. W. and COCHRAN, W. G. 1967. *Statistical methods*. The Iowa state Univ. Press, Ames, Iowa. 593 pp.

STEPHENSEN, K. 1948. Storkrebs. Ringkrebs. *Danm. Fauna, 53*: 1–187.

THOMASSEN, T. 1977. Comparisons of growth, fecundity and mortality between two populations of *Pandalus borealis* in Northern Norway. *Coun. Meet. int. Coun. Explor. Sea, 1977* (K:38): 1–6. 6 Tabs, 4 Figs. [Mimeo.]

THOMASSEN, T. and ULLTANG, Ø. 1975. Report from mesh selection experiments on *Pandalus borealis* in Norwegian waters. *Coun. Meet. int. Coun. Explor. Sea, 1975* (K:51): 1–6. 4 Tabs, 3 Figs. [Mimeo.]

ZAR, J. H. 1974. *Biostatistical analysis*. Prentice-Hall Inc. Englewood Cliffs, N. J. 620 pp.

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Table I. Station data. Code for trawls: PL: PL 1600-mesh shrimp trawl. Mesh size 35 mm. – NF: 1400-mesh NOFI sputnik shrimp trawl. Mesh size 35 mm. – CL: Campell Super 1400-mesh sputnik shrimp trawl. Mesh size 35 mm, but in addition a fine-meshed net was probably used. – GR: Granton bottom trawl with 22 mm net in cod end. – HT: Harstad pelagic trawl with 4 mm net in cod end.

*: In addition an 18 mm net was used.

a. *Stations taken with RV «G. O. Sars» in 1978.* (Cruises 1–78, 2–78, 4–78 and 5–78).

St.nr.	Date	Position	Depth (m)	Time	Dist-ance (nm)	Catch (kg)	Trawl type	Sample size	Numb. w. parasite
28	2/2	N 72°22' E 46°54'	250	12.35	3.0	260	GR	563	3
31	3/2	N 71°28' E 43°40'	248	20.50	3.0	90	GR	364	0
44	7/2	N 70°24' E 38°27'	205	05.35	3.0	51	GR	600	0
54	10/2	N 71°25' E 34°16'	226	19.45	2.9	20	GR	535	0
68	17/2	N 71°10' E 32°44'	248	15.45	2.8	15	GR	394	1
75	24/2	N 73°33' E 32°19'	296	13.40	3.0	75	GR	1081	1
77	25/2	N 72°19' E 31°24'	291	12.50	3.0	63	GR	672	0
79	1/3	N 72°06' E 32°37'	277	20.15	2.8	48	GR	343	0
80	3/3	N 72°08' E 30°11'	320	13.10	3.0	30	GR	369	0
111	20/4	N 73°42' E 24°30'	455	13.45	3.0	8	GR	514	0
116	22/4	N 72°56' E 24°30'	430	13.40	3.2	10	GR	143	0
140	23/6	N 71°21' E 30°42'	278	03.45	5.5	4	GR	361	0
147	26/6	N 72°00' E 40°00'	342	13.45	2.9	10	GR	467	0
362	1/9	N 72°00' E 32°20'	276	15.50	4.0	50	GR	455	1

b. *Stations taken with M.S. «Børvåg» in 1978.* (Cruise 3–78).

St.nr.	Date	Position	Depth (m)	Time	Dist-ance (nm)	Catch (kg)	Trawl type	Sample size	Numb. w. parasite
1	4/5	N 71°28' E 27°16'	380	07.30	1.4	178	PL	428	0
2	4/5	N 71°30' E 27°17'	380	09.45	5.0	105	PL	446	0
3	10/5	N 72°31' E 34°15'	280	06.30	6.0	400	PL	413	1
4	11/5	N 72°37' E 46°40'	270	08.45	2.5	362	PL	509	1
5	11/5	N 72°40' E 47°12'	270	11.40	5.0	335	PL	435	4
6	12/5	N 71°57' E 40°30	350	09.05	5.0	125	PL	466	0
7	12/5	N 72°02' E 38°42'	310	19.30	5.0	312	PL	437	3
8	13/5	N 72°31' E 34°15'	300	09.15	2.5	209	PL*	439	2
9	13/5	N 73°02' E 32°50'	250	16.40	2.5	25	PL*	456	1
10	13/5	N 73°02' E 32°50'	250	19.00	2.5	31	PL	420	1
11	14/5	N 73°30' E 33°00'	290	08.30	5.0	682	PL	437	1
12	14/5	N 73°13' E 32°07'	280	14.15	5.0	66	PL	397	0
13	15/5	N 72°30' E 31°37'	290	07.30	5.0	110	PL	409	1
14	15/5	N 72°28' E 30°14'	285	14.30	2.5	10	PL	429	1
15	15/5	N 72°43' E 28°45'	360	19.30	2.5	208	PL	409	1
17	16/5	N 72°17' E 28°39'	280	11.00	5.0	25	PL	445	1
18	16/5	N 71°54' E 29°10	300	17.15	5.0	110	PL	372	0
20	17/5	N 71°40' E 26°56'	370	08.10	5.0	480	PL	459	0
21	13/6	N 74°23' E 27°07'	404	13.25	5.0	150	PL	450	1
22	13/6	N 74°12' E 29°48'	364	20.30	5.0	118	PL	403	2
23	14/6	N 74°08' E 30°10'	346	07.10	5.0	110	PL	444	1
25	14/6	N 74°45' E 31°10'	330	17.30	5.0	175	PL	360	1

c. *Stations taken with M.S. «Finnmarkværing» in 1978.* (Cruise 6–78).

St.nr.	Date	Position	Depth (m)	Time	Distance (nm)	Catch (kg)	Trawl type	Sample size	Numb. w. parasit
8	20/10	N 76°26' E 30°22'	288	12.45	8.0	86	?	219	-
9	21/10	N 76°04' E 29°14'	270	09.05	6.0	198	?	209	-
10	21/10	N 75°58' E 28°58'	249	12.45	6.0	240	?	302	-
12	23/10	N 74°40' E 26°11'	295	12.00	8.0	85	?	299	-

d. *Stations taken with R.V. «G. O. Sars» in 1979.* (Cruise 1–79 and 4–79).

St.nr.	Date	Position	Depth (m)	Time	Distance (nm)	Catch (kg)	Trawl type	Sample size	Numb. w. parasite
20	23/1	N 72°00' E 45°53'	230	05.45	2.4	450	CL	267	0
21	24/1	N 72°00' E 40°34'	345	01.20	2.6	60	CL	461	3
24	25/1	N 69°12' E 37°39'	204	02.20	1.6	4	CL	213	2
25	26/1	N 71°30' E 34°00'	260	02.20	2.3	20	CL	227	2
35	14/2	N 72°35' E 32°43'	280	02.00	3.0	5	CL	205	1
36	15/2	N 71°55' E 32°53'	250	22.40	3.0	5	CL	216	0
38	15/2	N 71°35' E 32°20'	300	19.00	3.0	33	CL	438	0
40	19/2	N 70°40' E 33°20'	250	13.00	3.0	36	CL	431	3
41	20/2	N 70°06' E 34°45'	255	06.30	3.0	25	CL	386	2
43	23/2	N 70°36' E 32°50'	245	00.00	3.0	35	CL	278	0
52	2/3	N 71°01' E 29°18'	350	03.00	3.0	47	CL	113	0
160	15/7	N 75°57' E 30°30	320	16.35	2.3	275	CL	276	-

e. *Stations taken with M.S. «Stadhav» in 1979.* (Cruise 2–79 and 3–79).

St.nr.	Date	Position	Depth (m)	Time	Distance (nm)	Catch (kg)	Trawl type	Sample size	Numb. w. parasite
7	10/5	N 71°25' E 29°05'	344	06.20	5.0	150	PL	214	-
11	11/5	N 72°30' E 34°30'	277	09.55	3.0	100	PL	468	-
12	11/5	N 72°37' E 33°49'	306	13.20	5.0	250	PL	376	-
13	11/5	N 72°38' E 33°10'	301	16.45	5.0	260	PL	440	-
15	12/5	N 73°30' E 33°00'	296	10.00	3.0	15	PL	426	-
17	12/5	N 73°53' E 33°57'	324	17.10	6.0	160	PL	276	-
26	22/5	N 73°16' E 31°06'	324	07.30	5.0	230	PL	258	-
31	12/6	N 73°59' E 19°43'	400	15.45	6.0	300	PL	348	0
35	14/6	N 74°10' E 21°45'	252	15.05	6.0	250	PL	463	1
36	15/6	N 74°52' E 27°20'	324	18.30	3.0	50	NF	438	4
37	16/6	N 74°56' E 28°09'	343	07.10	3.0	90	NF	397	1
38	16/6	N 75°19' E 28°45'	340	12.50	3.0	70	NF	439	3
39	17/6	N 74°38' E 30°04'	364	07.45	5.8	280	NF	411	2
40	17/6	N 74°32' E 30°02'	354	10.55	8.0	380	NF	421	3
41	17/6	N 74°35' E 30°58'	301	17.05	6.2	160	NF	421	1
42	18/6	N 74°52' E 31°36'	272	08.00	4.0	15	NF	498	0
43	19/6	N 74°27' E 30°10'	349	15.40	6.0	150	NF	448	1
44	20/6	N 74°10' E 30°14'	349	07.10	6.0	225	NF	454	1
46	20/6	N 73°42' E 31°01'	385	23.40	3.0	75	NF	353	0
47	21/6	N 72°36' E 30°42'	288	08.30	6.0	300	NF	426	0
48	21/6	N 72°24' E 31°46'	288	13.20	8.0	220	NF	393	0
49	21/6	N 72°35' E 33°09'	293	19.45	3.0	15	NF	390	2
50	22/6	N 71°50' E 32°10'	310	07.30	6.0	550	NF	475	0
51	22/6	N 71°54' E 31°30'	328	11.35	6.0	120	NF	410	3
52	22/6	N 71°58' E 31°46'	313	16.10	6.0	385	NF	501	0
53	23/6	N 71°44' E 27°35'	342	07.10	3.0	80	NF*	452	0

f. *Pelagic stations taken with R/V «G. O. Sars» and R/V «Johan Hjort» in 1978.*

St.nr.	Ship	Date	Position	Depth (m) Trawl	Bottom	Catch (kg)	Dist-ance (nm)	Trawl type	Samp size
42	G.O.Sars	6/2	N 71°40' E 39°25'	60	372	½	1.5	HT	78
57	G.O.Sars	11/2	N 72°10' E 36°54'	96	248	2½	0.8	HT	460
446	G.O.Sars	22/9	N 75°49' E 35°00'	40	219	6	1.4	HT	434
459	G.O.Sars	26/9	N 72°38' E 32°40'	25	276	20	1.0	HT	297
466	G.O.Sars	30/9	N 72°37' E 39°46'	30	322	25	1.0	HT	423
468	G.O.Sars	1/10	N 75°27' E 43°00'	40	300	6	1.5	HT	370
477	G.O.Sars	3/10	N 76°00' E 45°00'	30	228	10	1.2	HT	517
378	Johan Hjort	20/9	N 75°09' E 27°00'	15	239	10	1.1	HT	404