J. mar. biol. Ass. U.K. (1959) 38, 189–220
Printed in Great Britain

ON THE BIOLOGY OF *PANDALUS BOREALIS* KRØYER, WITH REFERENCE TO A POPULATION OFF THE NORTHUMBERLAND COAST

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(Text-figs. 1–14)

The deep sea prawn, *Pandalus borealis* Krøyer, is fished extensively in Norwegian, Swedish and Greenland waters, some 4000 metric tons being caught annually, having a value of about £800,000. Its biology has been investigated by various workers in these countries. Comprehensive accounts have been given by Wollebaek (1903), Hjort & Ruud (1938), Rasmussen (1953) and Horsted & Smidt (1956). Despite this, relatively few populations have been sampled at regular intervals throughout a year. In high latitudes where much work has been carried out, ice, for varying lengths of time, prevents stocks from being sampled. Rasmussen (1942, 1949, 1953) has shown that the life history of *P. borealis* varies with locality in a range from southern Norway to Spitsbergen. When *P. borealis* was found in numbers in deep water off the Northumberland coast advantage was taken to investigate the biology of the species at the southern limit of its eastern Atlantic distribution and to compare the results with those of other workers. Knowledge of the biology of the prawn now covers the whole of its north-south distribution and some account of this is given. In addition, the study gives information on a population that has not been fished commercially and provides a more complete picture of sex reversal than has been obtained hitherto.

I am particularly indebted to Dr A. Ritchie of the Scottish Home Department Laboratory, Aberdeen, who has allowed me to use his data on the distribution, size and sex of *P. borealis* in British waters. I am also indebted to Dr H. O. Bull for many suggestions, for records of distribution and for temperature and salinity data. I wish to thank Mr R. Harrison, skipper of the R.V. 'Alexander Meek' for collecting in all weathers, and my wife for her criticism.

DISTRIBUTION

P. borealis occurs in both Pacific and Atlantic oceans (Fig. 1). Ekman (1953) refers to it as having a discontinuous north Atlanto-Pacific distribution and as a discontinuous circum-*boreal* species. Earlier records of its distribution are given by Rathbun (1904) and Hofsten (1916), the latter giving detailed

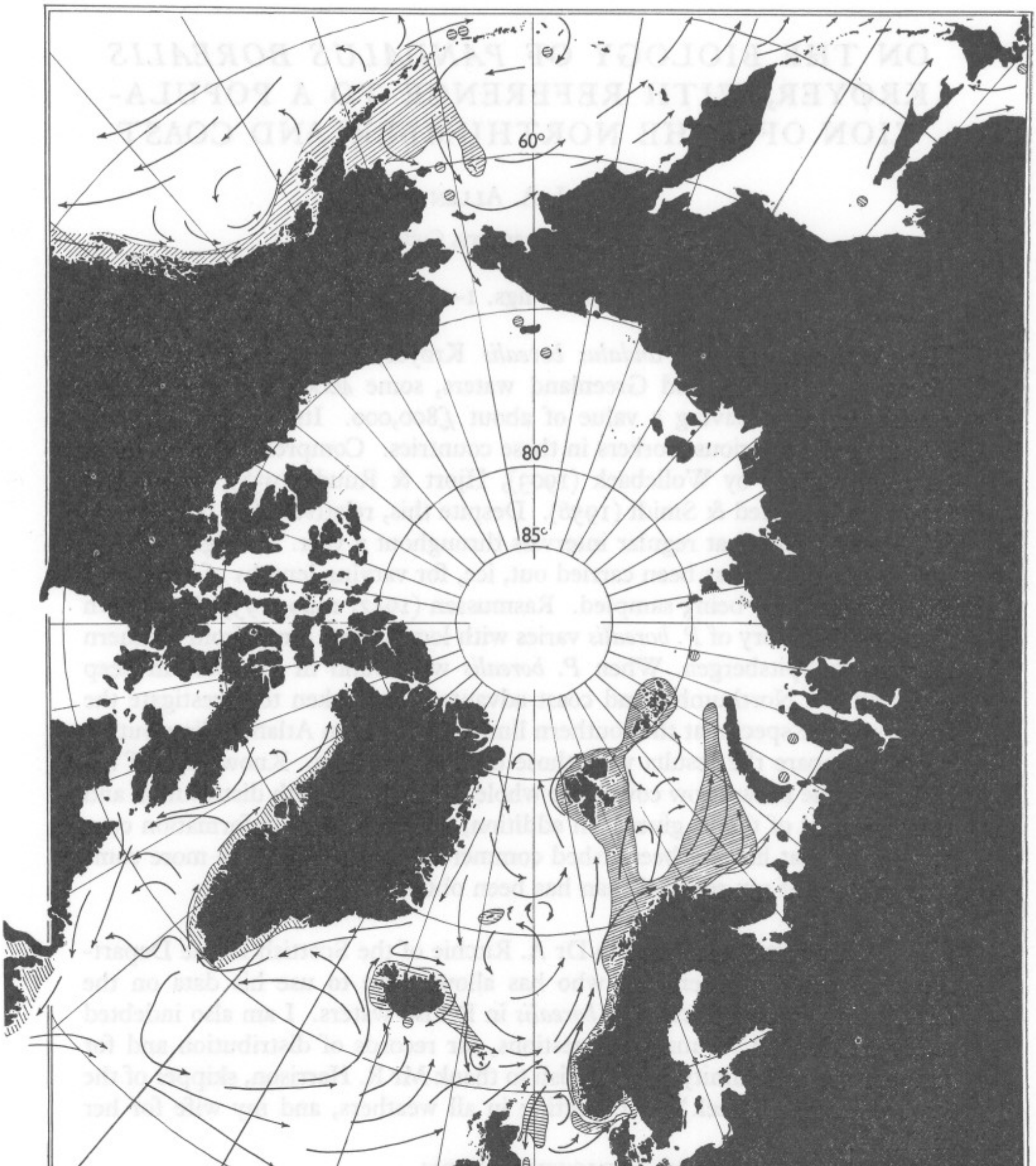

Fig. 1. Distribution of *Pandalus borealis* (shaded areas) Arrows indicate the general direction of flow of the surface currents. Records of Berkeley (1930), Blacker (1957), Bjørk (1935), Gorbunow (1934), Grieg (1925, 1926*a*, *b*, 1932), Heegaard (1941), Hjort & Ruud (1938), Hofsten (1916), Horsted & Smidt (1956), Hynes (1929), Johnson & Lindner (1934), Poulsen (1946), Pruter & Harry (1952), Rasmussen (1942, 1953), Rathbun (1904, 1929), Sivertsen (1932), Stephenson (1935) and the present work.

maps and references. The present maps (Figs. 1, 2) bring knowledge of its distribution up to date, the authorities being listed in the legends to the figures.

Knowledge of the distribution of the prawn in the Pacific and off the eastern seaboard of America has been little extended since the work of Rathbun (1904). Rathbun (1929), Hynes (1929), Berkeley (1930), Johnson & Lindner (1934) and Hjort & Ruud (1938) all refer to its distribution but give few new localities. *P. borealis* is common off the coasts of Alaska and to the south as far as the Columbia River (lat. 46° N.). It is also common in the eastern part of the Bering Sea and off the Aleutian Islands. To the north of the Bering Straits it has been recorded in latitude 73° off Vrangelye Island. It is much less common off the western coasts of the Pacific but is reported from Japanese waters at least as far south as latitude 45° N. In the eastern Atlantic *P. borealis* occurs in large numbers in the Gulf of Maine and off Cape Cod. The most southerly record is in latitude 41° N. There is a curious lack of records between Cape Cod and the southern tip of Greenland (Fig. 1), although it has been presumed to occur (Johnson & Lindner, 1934; Hjort & Ruud, 1938). On the west coast of Greenland there are dense populations supporting a lucrative fishery (Horsted & Smidt, 1956), but there are no records of its occurrence on the west side of the Davis Strait (see p. 194). Miss V. Brawn of St Andrews Biological Station, N.B., Canada, in a personal communication, states that it is present in the Gulf of St Lawrence but has no record from farther north.

Large populations of *P. borealis* occur in eastern Atlantic waters off the Norwegian coast and as far north as Franz Josef Land (lat. 82° N.), but no farther east than longitude 79° E. They occur off the east coast of Greenland as far north as latitude 66° N., and off the coasts of Spitsbergen, Jan Mayen, Iceland and the Faroes. To the south of Norway the prawn is present in the Skagerak and Kattegat, but no farther south than latitude 56° N. It occurs in deep water (>80 m) in the North Sea (Fig. 2). A single specimen has been recorded from south of the Dogger Bank in latitude 54° 24′ N. (Wedmeyer, 1912), but it is doubtful whether there is any permanent population south of latitude 55° N. *P. borealis* was first recorded off the Northumberland coast north-east of Coquet Island by Todd in 1907 (Norman & Brady, 1909). A specimen taken off the Scottish coast in 1904 by the 'Michael Sars' (Grieg, 1926*b*, see Appendix I) appears to be the first British record. Neither Bell (1853) nor Calman (1899) list *P. borealis*. Although Jorgensen (1923) records larvae as present in plankton samples from the Northumberland area this is probably incorrect (see p. 208). As yet there is no published record of larvae being taken from the North Sea by continuous plankton recorder surveys (Rees, 1952, 1955). Through the kindness of Dr I. Gordon, Dr A. Ritchie and Dr H. O. Bull unpublished records from British waters from 1930 to the present date are available (see Appendix I).

Information on *Pandalus borealis* is sufficiently complete to give a reliable picture of its ecology over the whole of its eastern Atlantic distribution. Temperature, salinity, substratum, and, possibly, depth are limiting factors in its distribution. Adult prawns have been taken from water with temperatures ranging from – 1·68° to 11·13° C (Fig. 3). Horsted & Smidt (1956) have

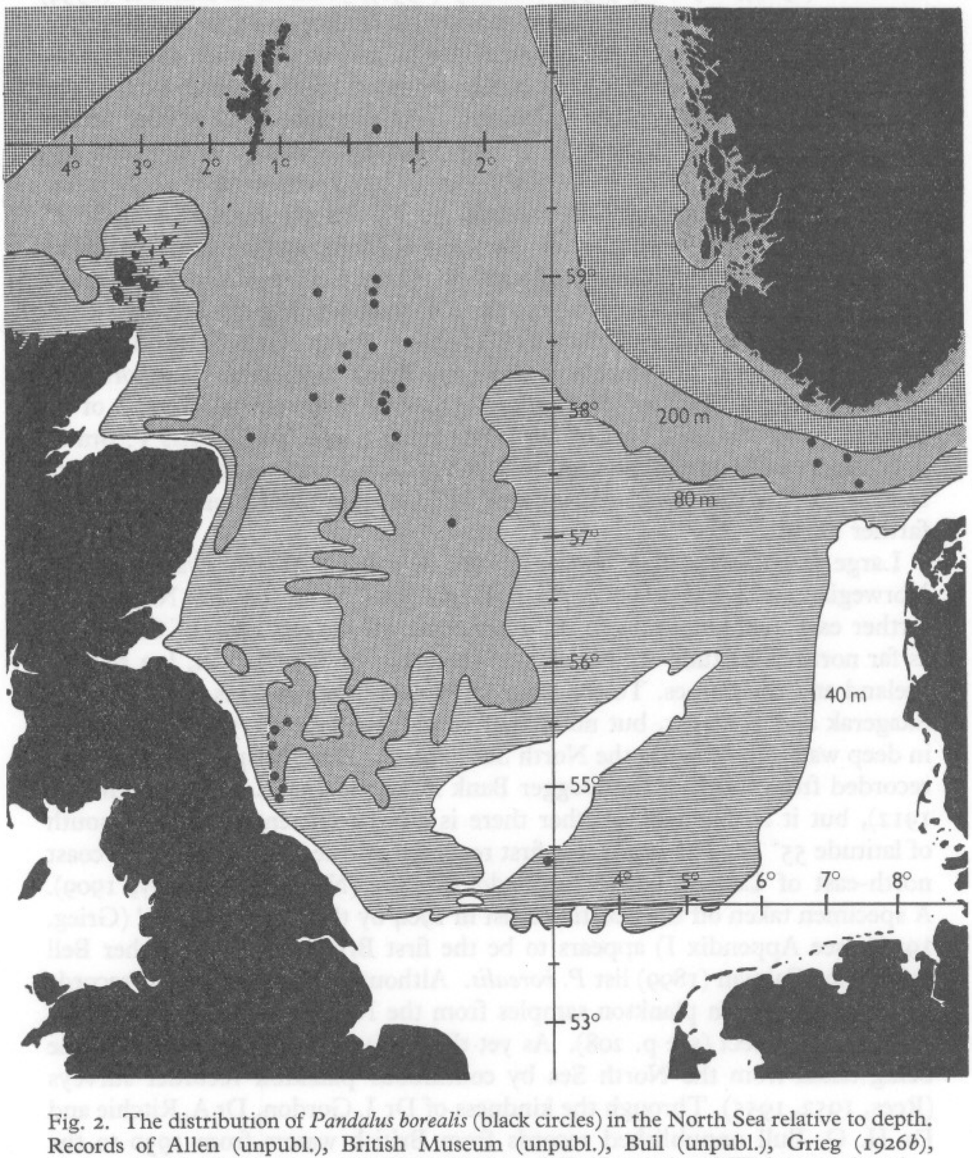

Fig. 2. The distribution of *Pandalus borealis* (black circles) in the North Sea relative to depth. Records of Allen (unpubl.), British Museum (unpubl.), Bull (unpubl.), Grieg (1926*b*), Poulsen (1946), Ritchie (unpubl.), Todd (Norman & Brady 1909) and Wedemeyer (1912).

shown that prolonged (2 months) temperatures of less than -1° C are deleterious to prawns and caused mass mortality in the stocks at Holsteinborg during 1948–49 with the consequent failure of the fishery for the following 5 years. Ekman (1953) refers to *P. borealis* as a boreal species (as its name suggests) and presumes that it owes its existence in high arctic waters to transport from warmer regions, notably by means of the Gulf Stream and the North Atlantic Drift. He questions whether the species can propagate in high latitudes. While it undoubtedly owes its existence in high arctic waters to the north-east of Spitsbergen and the north of Novya Zemlya to the warm North Atlantic current, Rasmussen (1942) has shown that the Spitsbergen population reproduces. Similarly, populations off the West Greenland coast (lat. 75° N.) at temperatures close to limiting also reproduce (Horsted & Smidt, 1956). It is a true arctic-boreal species with little or no 'sterile expatriation area'. There is little doubt that the extremely cold water of the Labrador current is one factor that prevents the establishment of stocks on the west side of the Davis Strait. Temperature is probably the most important factor limiting distribution in high latitudes. It has been assumed that the upper limiting temperature is 8° C (Rasmussen, 1953, and others), although Poulsen (1946) showed that adults can live at 9·5° C and schizopod stages at 14° C in Danish waters. The present study shows that the adults can live and breed in temperatures as high as 11·1° C. The range in temperature of the water of the prawn grounds off the Northumberland coast during the present investigation was from 6° to 11·1° C and during the period July to December was 9° C or above. There are no records of temperatures at the southern limit of distribution off the Pacific and Atlantic coasts of America, but general charts, e.g. Schott (1942), indicate temperatures of approximately 8° C. It

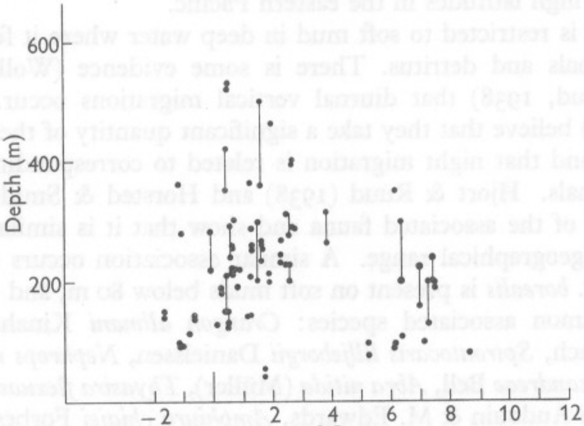

Fig. 3. Records of the depths of various populations of *Pandalus borealis* plotted against temperature of their environment. Authorities as listed in the legend to Fig. 1.

appears likely that *P. borealis* off the Northumberland coast is living at the extreme upper limit of its temperature range. Apart from Poulsen (1946) who records larvae from water at 14° C in the Kattegat, there are no records of a high temperature sterile expatriation area.

Adult *P. borealis* are restricted to water of fairly high salinity. Although Poulsen (1946) found larval stages in salinities of 32‰, only in Oslo Fjord (33–33·6‰; Hjort & Ruud, 1938) has the prawn been recorded in salinities of less than 34‰. All other records range from 34·1 to 35·7‰ and only two records exceed 35‰. The salinity of the deep water off the Northumberland coast varies from 34·47 to 34·87‰. The species is stenohaline, therefore salinity, in addition to temperature, must limit its spread along the Labrador coast and in high latitudes in the eastern Pacific.

P. borealis is restricted to soft mud in deep water where it feeds on small bottom animals and detritus. There is some evidence (Wollebaek, 1903; Hjort & Ruud, 1938) that diurnal vertical migrations occur. Horsted & Smidt (1956) believe that they take a significant quantity of their food above the bottom and that night migration is related to corresponding migrations of food animals. Hjort & Ruud (1938) and Horsted & Smidt (1956) give detailed lists of the associated fauna and show that it is similar throughout the prawn's geographical range. A similar association occurs in the North Sea. Here *P. borealis* is present on soft muds below 80 m, and the following are the common associated species: *Crangon allmani* Kinahan, *Pandalus montagui* Leach, *Spirontocaris lilljeborgii* Danielssen, *Nephrops norvegicus* L., *Calocaris macandreae* Bell, *Abra nitida* (Müller), *Thyasira flexuosa* (Montagu), *Glycera rouxi* Audouin & M. Edwards, *Amphiura chiajei* Forbes.

Distribution in depth varies from 20 to 900 m, but most records fall between 80 and 650 m. Records taken from Rasmussen (1953) and Horsted & Smidt (1956) show that the higher the latitude the deeper is the densest population. Few prawns are found in the deepest water (>600 m) of the Skagerak, although conditions appear suitable (Poulsen, 1946). The most suitable substrata may not necessarily be in deeper water in the north. Salinity and temperature will be as significant as type of substratum in determining the depth of the population. Thus values of temperature and salinity are relatively high and constant in deep water (350–600 m) in high latitudes, while in shallower water limiting values may be exceeded.

There is a relationship between the distribution of *P. borealis* and the warm current systems (Fig. 1). Horsted & Smidt (1956) show that its distribution on the west coast of Greenland is closely related to the Irminger current. There is clear correlation between the eastern Atlantic populations and the ramifications of the Gulf Stream and also between the eastern Pacific populations and the warm northerly coastal currents off the west coast of America. The prawn does not occur west of the Orkney–Shetland channel in British waters, and it is possible that the North Sea stocks originate from Faroe or

Norwegian populations (Fig. 1). There appear to be suitable grounds for *P. borealis* off the west coasts but it is possible that the larvae are restricted to the northern fringe of the Gulf Stream and will not be carried to these waters.

METHODS

The prawns used in this study were all obtained from the same position—13 nautical miles east of Blyth harbour entrance. A 9 ft beam trawl fitted with a King's Lynn type prawn trawl was used. All hauls were of 20 min duration, the same trawl being used throughout the work. The position worked is also a hydrographical station, and Dr H. O. Bull has kindly allowed his records to be used. Many of the latter were taken at the same time as the prawn haul.

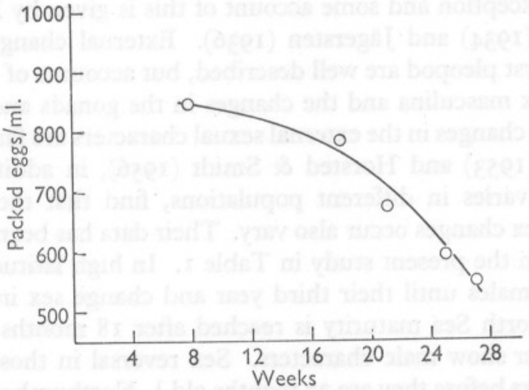

Fig. 4. Numbers of packed eggs/ml. (see text) plotted against age of the eggs.

The catch was examined alive and sorted. *P. borealis* was fixed in 4% neutral formalin in sea water and later transferred to 70% alcohol. All specimens were sexed and the carapace length from the posterior limit of the eye socket to the extreme posterior lateral edge of the carapace measured. Measurements were taken to the nearest millimetre. The correction factor for this population, that figure which when multiplied with carapace length gives total length, is 5·05 (extreme limits 4·8–5·2). This is a higher factor than that of Horsted & Smidt (1956). The latter using the same measurement of carapace obtained a factor of 4·6–4·7.

Eggs, when present, were counted, sized and examined for degree of development. The method used for counting was that of Rasmussen (1953). Eggs of a small number of specimens were counted and then hand-centrifuged in a calibrated tube and the packed egg volume noted. A conversion factor (packed eggs/ml.) is calculated and the egg numbers of the remaining specimens derived from packed egg volumes. As the egg volume increases with increasing age (Fig. 4), a new conversion factor has to be calculated for each sample.

Specimens, male, female and intersex, were selected from each size-group of each sample and the secondary sexual characters examined. The endopodite of the first pleopod, the appendix interna of the second pleopod and appendix masculina, if present, were drawn accurately with the aid of a squared eye-piece graticule. The same objective and eyepieces (magn. × 5 and × 10 respectively) were used throughout the work. Gonads from the selected specimens were removed for sectioning and the sections stained with Mallory's Triple Stain, and Eosin and Fast Green.

SEX REVERSAL AND GAMETOGENESIS

Most *Pandalus* species are protandrous hermaphrodites (Berkeley, 1930; Kubo, 1951; Pike, 1952; Pruter & Harry, 1952; Mistakidis, 1957). *P. borealis* is no exception and some account of this is given by Berkeley (1930), Leopoldseder (1934) and Jägersten (1936). External changes in the endopodite of the first pleopod are well described, but accounts of changes in form of the appendix masculina and the changes in the gonads and the relation of the latter to the changes in the external sexual characters are far from complete.

Rasmussen (1953) and Horsted & Smidt (1956), in addition to showing that life span varies in different populations, find that the ages at which maturity and sex changes occur also vary. Their data has been compared with that obtained in the present study in Table 1. In high latitudes prawns may not mature as males until their third year and change sex in the sixth year, while in the North Sea maturity is reached after 18 months and more than 30% may never show male characters. Sex reversal in those showing male characters occurs before they are 27 months old.[1] Northumberland prawns do not live for more than 38 months. Table 1 shows that intermediate populations (Eids, Ofoten and Mist Fjords) are also intermediate in respect of their age at maturity and at sex change. Thus the life history of the North Sea population most closely resembles that of the Oslo Fjord population. Hjort & Ruud (1938) found in the latter population that approximately 5% never function as males.

Hjort & Ruud (1938), discussing sex change in the southern Norway populations, suggest a 'labile equilibrium' between male and female potentialities where the age of female maturity depends on the age at which the male tendencies are repressed. Jägersten (1936) from work on *P. borealis* from Gullmar Fjord suggests that all individuals are hermaphroditic and have both male and female potentialities. Jägersten recognizes three categories: (1) primary females, in which potentiality is repressed so early that male characters never appear; (2) secondary females, in which male potentiality is repressed soon after male characters have appeared (these animals mature as females in their second year); and (3) hermaphroditic females, in which male potentialities are repressed after functioning as a male. Rasmussen (1953) shows a

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[1] The age of the prawns is calculated from the date at which all the larvae are hatched, i.e. the end of the second week in April (see p 206).

definite relationship between size, maturity and sex (see Table 1); normally prawns less than 70 mm total length at the breeding season are immature, while those greater than 115 mm total length are females. Few prawns above 110 mm total length function as males and only a few mature females were recorded below 90 mm. Rasmussen (1953) was able to predict the percentage of immature, males and females from the size range of the age-group at the beginning of the breeding season. The size range of the North Sea prawn at the commencement of the first breeding period (1½ years) is 76–96 mm and approximately 35% are primary or secondary females (see p. 196), i.e. a much higher proportion than the 5–10% predicted from Rasmussen's data. As Rasmussen (1953) points out, variations in relationship can be found in different localities, although it seems likely that this particular variation is significant. In the Northumberland population the slight increase in the

TABLE 1. PERCENTAGE COMPOSITION OF POPULATIONS OF *PANDALUS BOREALIS*

The percentages of immature, mature male and mature female *P. borealis* at the breeding seasons of various populations. Total length measurements in mm are given in parentheses. Scandinavian data extracted from Rasmussen (1953) and Horsted & Smidt (1956).

Locality	Age yr.	% immature (length)	% mature ♂ (length)	% mature ♀ (length)
1. Northumberland	1½	—	63·5 (76–90)	36·5 (81–96)
2. S. Norway		—	82–99·5 (80–94)	0·5–18 (90–101)
3. Eids and Ofoten Fjords		0–0·2 (58)	99·8–100 (58–85)	—
4. Mist Fjord		100 (50)	—	—
5. W. Greenland and Jan Mayen		100(49)	—	—
6. Spitsbergen		100 (40)	—	—
1. Northumberland	2½	—	—	100 (100–126)
2. S. Norway		—	0–78·5 (96–111)	21·5–100 (120–130)
3. Eids and Ofoten Fjords		—	16–88·5 (92)	11·5–84 (100–103)
4. Mist Fjord		—	100 (77)	—
5. W. Greenland and Jan Mayen		100 (69)	—	—
6. Spitsbergen		86–99 (64)	1–14 (78)	—
2. S. Norway	3½	—	—	100 (130–140)
3. Eids and Ofoten Fjords		—	—	100 (122–143)
4. Mist Fjord		—	100 (96)	—
5. W. Greenland and Jan Mayen		—	100 (94)	—
6. Spitsbergen		—	100 (87)	—
2. S. Norway	4½	—	—	100 (150–159)*
3. Eids and Ofoten Fjord		—	—	?*
4. Mist Fjord		—	—	100 (113·5)
5. W. Greenland and Jan Mayen		—	71 (115)	29 (126)
6. Spitsbergen		—	100 (104)	—
4. Mist Fjord	5½	—	—	100 (120)
5. W. Greenland & Jan Mayen		—	—	100 (139)
6. Spitsbergen		—	—	100 (118)
6. Spitsbergen	6½	—	—	100 (121)
6. Spitsbergen	7½	—	—	100 (140)
6. Spitsbergen	8½	—	—	100 (> 140)*

* Very few specimens.

number of females during the first 18 months of the life of the year group (Fig. 5) corresponds with sex reversal to secondary females. Although it is the largest of the immature male prawns of each sample that show reversal, there does not appear to be a minimum size below which reversal does not take place. Increased growth rate, rather than the attainment of a certain size, appears to be related to sex reversal. Observations support a theory of hormonal control (see pp. 205 and 214).

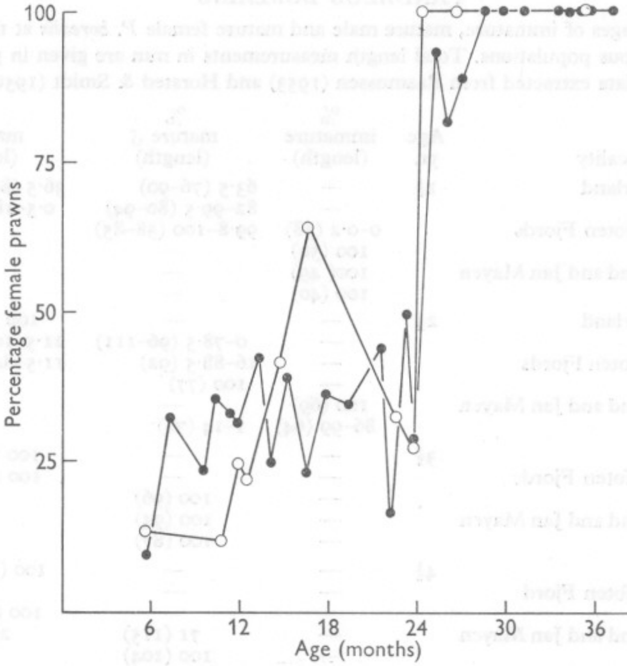

Fig. 5. The variation in the percentage of female *Pandalus borealis* during the life of a year group. Calculated from Northumberland (dots) and Scottish data (rings).

It might be expected that where late reversal of sex takes place both eggs and sperm may be produced by the same animal at 18 months. No prawn was taken that carried eggs and also possessed male external sexual characters, but sections of one prawn, 14 months old, male, with the terminal setae of the appendix masculina slightly shorter than normal, showed proliferating oocytes as well as primary spermatocytes (see p. 204). Similarly, reversal might be so retracted in the case of a male that the prawn acts as a male for a second time at 2½ years. Hjort & Ruud (1938) report four such animals from southern Norway, all very large specimens 116–126 mm. Two specimens showing unmodified external male sexual characters 4 months after egg-laying were taken, but sections of the gonads showed that oocytes only were present. It is unlikely that specimens of the Northumberland population act twice as males.

Secondary sexual characters

The change in form of the endopodite of the first pleopod and the appendix interna and appendix masculina of the second pleopod that occurs with sex reversal in the Northumberland population is shown in Fig. 6. The endopodite and appendix interna of the primary females (outlined, but not hatched) gradually increase in size throughout the life of the prawn. There is little change in shape, only the tip of the endopodite becoming more attenuated with age. The form and arrangement of the setae are not shown. 'Breeding dress' is assumed at the moult preceding egg-laying. In this condition the setae are numerous, long, feathery and adapted for the attachment of eggs. Høglund (1943) gives an excellent description of the change. In Fig. 6 those pleopods shown stippled are drawn from prawns in breeding dress.

The male endopodites (black in Fig. 6) bear the copulatory organ which projects just below the apex. A number of small hooks or cincinnuli are present on the tip of the organ, 4–6 in young prawns and more than 10 in older specimens. Below the copulatory organ are 3 or 4 small spine-setae and the remainder of the setae on the endopodite are typically long and pinnate. The above details are very similar to those described by Mistakidis (1957) for *P. montagui*. In young prawns the copulatory organ is relatively long and slender and extends beyond the apex. In older males the organ is considerably broader in relation to its length and barely extends beyond the more defined apex. The male endopodite is somewhat larger than that from a female of the same age, the change in shape with age being shown in Fig. 6. The appendix masculina, situated between the side of the endopodite of the second pleopod and the appendix interna, was present in all male prawns and no difficulty was experienced in sexing the youngest specimens. The appendix masculina of 6-month prawns is a small rounded projection bearing two or three small apical setae. The projection grows rapidly in length and by 12 months is almost as long as the appendix interna, the number of setae increasing to five terminal and three lateral. The setae are almost as long as the appendix masculina itself. Maximum size is reached at about 16 months. Atrophy occurs after the sperms have been released.

The form of the external characters of the males after spawning may change at 22 months or as late as 28 months (Fig. 6 hatched appendages). The copulatory organ becomes progressively thinner and the apex of the endopodite more pointed. There appear to be three transitional stages before the copulatory organ is finally lost. In many specimens the tip of the organ is lost at the third stage, the base remaining. The appendix masculina is slower to disappear than the copulatory organ and at least one extra moult is necessary before it too is lost, i.e. at least five moults are required for the complete reversal of the external male characters. The first indication of change in the appendix masculina is reduction in size and number of the setae, followed by the

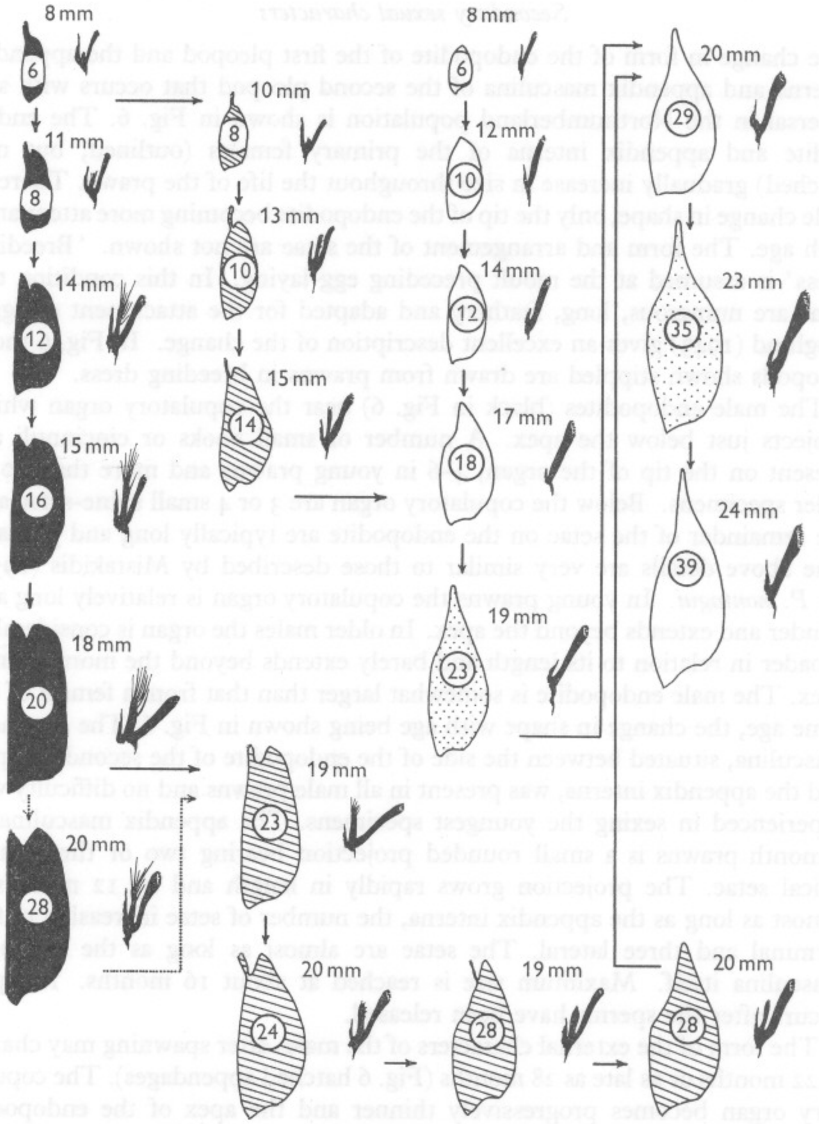

Fig. 6. To show the changes in form with increasing age of the endopodite of the first pleopod and the corresponding appendix interna and appendix musculina of the second pleopod of *Pandalus borealis* from the Northumberland population. Age in months is given in the ring in each endopodite and the carapace length (mm) above each figure. Male endopodite, black; transitional, cross-hatched; female, outlined; those in breeding dress, stippled. Arrows indicate sequence.

gradual reduction in size of the appendix. Transition stages in immature prawns were found on re-examination of Northumberland samples. The youngest was 8 months old. A similar series of stages were found to those described above, although the appendix masculina never becomes fully setose (Fig. 6).

Histology of gonads

The general morphology of the gonads has been described by Wollebaek (1903), Berkeley (1930), Leopoldseder (1934) and Jägersten (1936). They are elongate, paired, tubular structures joined by a bridge about a third the distance from the anterior end. The vas deferens and oviduct join the gonad mid-laterally, the oviduct being anterior to the vas deferens (Berkeley, 1930, p. 130). Sections, mainly transverse, were cut from some 70 gonads representative of all ages and external sexual characters. The maximum oocyte diameter was recorded for each gonad to give information on oocyte growth (Fig. 7).

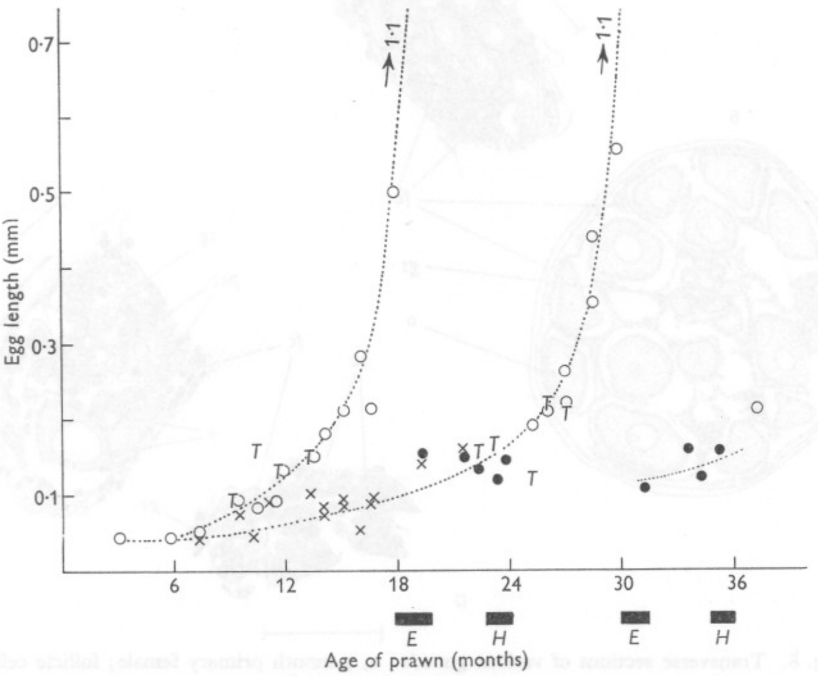

Fig. 7. Graph to show the increase in length of the oocytes (dotted line) with the age of the prawn. The plotted lines may be continued upwards linearly, and at a size of about 1·1 mm the oocytes have developed into eggs. The symbols indicate the sex of the prawns; ●, female carrying eggs on the pleopods; ○, female not carrying eggs; × male; *T*, transitional; *E*, egg-laying; *H*, hatching of larvae.

Primary females. The maximum oocyte diameter of the youngest female prawn taken (3 months) was 0·04 mm. The oocytes occupy approximately half the ovary. The remainder of the ovary is filled with small cells which are probably early follicle or interstitial cells. Aoto (1952) describes a similar condition in *Pandalus kessleri*. The proliferating strand of oocytes is not central but on the inner, ventral side of the gonad. During the next 3 months there is little increase in oocyte size but proliferation continues until much of the ovary is filled. There appear to be fewer interstitial cells, but this may possibly be due to the attenuation of their cytoplasm and new arrangement.

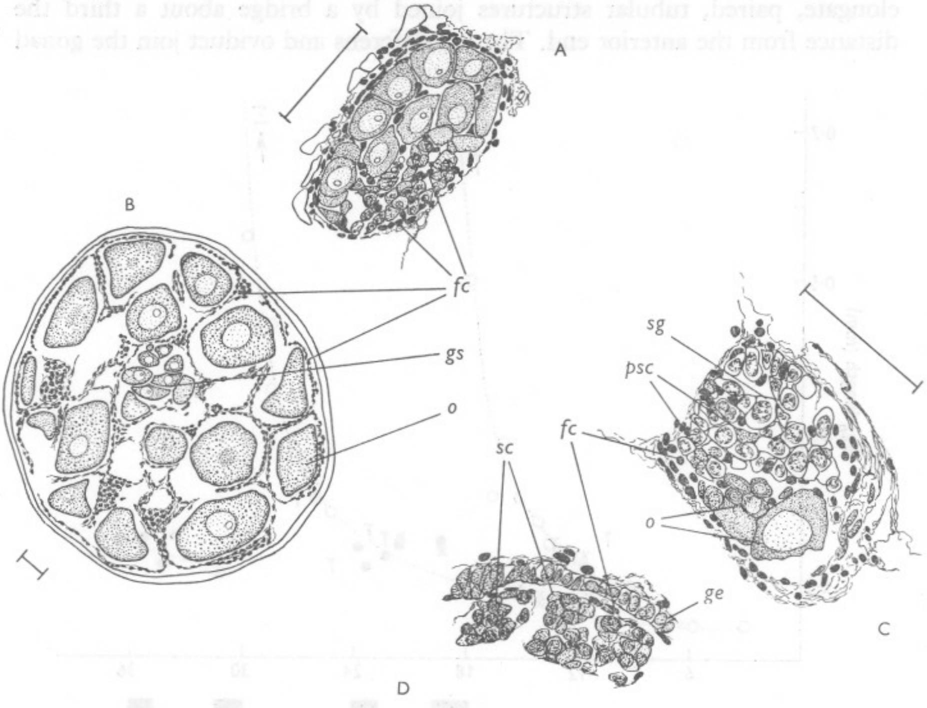

Fig. 8. Transverse sections of various gonads. A, 7-month primary female; follicle cells at oocyte interstices. B, 27-month female; a single layer of follicle cells surrounding each oocyte. C, 7-month hermaphrodite female; oocytes occupy ⅓ of gonad, the spermatogonia are not grouped. D, 15-month hermaphrodite female; a small part of the periphery of the gonad showing two groups of spermatocytes close to the gonadial epithelium with follicle cells beginning to surround each group. *fc*, follicle cell; *ge*, gonadial epithelium; *gs*, germinal strand; *o*, oocyte; *psc*, 'primary sex cell'; *sc*, grouped spermatocytes; *sg*, spermatogonia. Each scale represent 0·1 mm.

In prawns 7 months old the walls of the gonad are lined with a layer of follicle cells while others surround the developing oocytes (Fig. 8). The nuclei of the follicle cells stain heavily, while the 'attenuation' of the cytoplasm makes it impossible to distinguish any cell walls. Oocytes are still being proliferated, the largest are peripheral and 0·05 mm long. The oocytes are angular with the follicle cell nuclei in the interstices. In 9-month primary females growth rate of the oocytes increases, although the general appearance of the ovary remains the same. The rate of proliferation of oocytes is maintained, the gonad increasing in diameter until the prawn is 11½ months old when the rate begins to drop. By this time the largest eggs are 0·15 mm long and small vacuoles appear in the cytoplasm. The interstitial cells show no change in appearance, but the germinal strand, while still asymmetrical, is more centrally placed. The oviduct is still a narrow tube. Acceleration of the growth rate of the oocytes continues, reaching a maximum rate in the 16-month prawn and this rate is maintained until the eggs are laid. At 16 months yolk granules appear and the oocytes are more rounded. The largest recorded oocyte diameter was 0·5 mm. This was recorded from a prawn in a sample in which most females had laid their eggs. During the last few days before laying or perhaps immediately after laying the oocyte must more than double its diameter as the smallest newly hatched eggs measure 1·1 mm (maximum diameter). The cytoplasm of the follicle cells of 16-month old females is better defined and the number of cells increases. The germinal strand remains after the eggs are laid and a number of small oocytes remain close to it. The largest remaining oocytes (0·15 mm) quickly take up a peripheral position where they are surrounded by the now very well-developed follicle cells. The latter, both round the oocytes and lining the ovary epithelium, are two or three layers thick. From the release of the mature eggs (about 18 months) until the 24th month little change occurs in the ovary. The follicle cells if anything increase slightly but the number of oocytes appears to remain constant. The remaining oocytes do not grow and show no sign of disintegration. Prior to the larvae hatching, the follicle cells decrease in size and number. The central cells are the first to return to the 'resting state', those at the periphery remain prominent until after the larvae are hatched, i.e. 25 months. At this time the remaining oocytes start to grow again and proliferation of new oocytes recommences. In 27-month-old prawns yolk is appearing in the large peripheral oocytes (0·22 mm max. diam.) and a similar cycle of events to that described follows. Maximum growth of the oocytes is reached when the prawn is 28 months old and by this time there is little proliferation of new cells, although the germinal cord surrounded by small cells remains. The maximum recorded oocyte size was 0·53 mm in a 30-month-old prawn. Egg laying commences at 30½ months. As before, only those eggs more than 0·15 mm are released, and the follicle cells again are greatly developed. The largest remaining oocytes take up a peripheral position surrounded by follicle cell layers. There is no further proliferation of oocytes and at 33 months the first sign of disintegration is seen. The prominent nucleolus is lost and the nuclear membrane is no longer clearly defined. By the 35th month the cell walls of the oocytes have broken down and the follicle cells are reduced.

As before, the latter are well developed while the eggs are carried on the pleopods.

Hermaphrodite females. All prawns showing external male characters have an ovarian germinal strand, together with a few oocytes which occupy between a quarter and a third of the area of the gonad in cross-section. The oocytes are in the 'mature' condition (Berkeley, 1930) having a clear nucleus, well-developed nucleolus and an enlarged heavily staining cytoplasm. The ovarian portion is acentric occupying a dorso-lateral position. The maximum oocyte size in the smallest prawns (5½–7 months old) was 0·04 mm. In these specimens, spermatogonia filled the rest of the gonad and although the cells are tightly packed there is no definite tubule structure (Fig. 8). The nuclei show the typical 'bouquet' stage of actively dividing primary and secondary spermatogonia described by Runnström (1925) with clumps of chromatin material at the periphery. Follicle cells line the gonadial walls, and typically, the oocytes, and there are a few scattered between the spermatogonia. A few cells among the latter stain heavily with the acid fuchsin of Mallory's Triple Stain and these probably correspond with the 'primary sex cells' described by Berkeley (1930). Sections show little change until after the prawns are 11 months old. By the 13th month spermatocytes are present. The gonad is larger and the oocytes still occupy about a third of the gonad. There has been some proliferation of oocytes to maintain the relative proportions and there is slight growth of the outer oocytes (0·08 mm max. diam.). Spermatogonia are still present close to the oocytes as a tight packed mass, but peripherally the cells are no longer in the 'bouquet' stage and are lighter staining than the latter. There is no obvious tubular arrangement and follicle cells are scattered between the spermatocytes. In a 14-month-old prawn the peripheral spermatocytes appear to be divided into groups. Although a few follicle nuclei are present between the groups the latter do not appear to be surrounded by the follicle cells (Fig. 8). The tenuous nature of the follicle cell's cytoplasm makes it difficult to determine this with any surety. Berkeley (1930) refers to this cytoplasm as a 'plasma without cell walls'. By 16 months the peripheral groups are clearly surrounded by follicle cells. While there are still many densely packed spermatocytes close to the oocytes, much of the testis is filled with the groups of larger spermatocytes. During the next month sperms are produced. These are of the typical four-rayed type. At the same time there is a great increase in the number of follicle cells. As yet there are no sperms in the vas deferens, but by 18 months most of the sperms have been transferred and the follicle cells surrounding the remaining spermatocytes increase further. The remaining spermatocytes are the remnants of those that were close to the oocytes. The oocytes, also surrounded by follicle cells, proliferate rapidly and the peripheral oocytes have grown to 0·15 mm (max. diam.). By 21½ months fertilization has occurred and the immature oocytes nearly fill the gonadial cavity. The walls of the gonad are very thick and this is due in part to follicle cells and in part to the remains of what appear to be spermatocytes. A similar condition is reported by Aoto (1952) for *P. kessleri* and by Fasten (1926) in the crab *Lophopanopeus bellus*. Both these authors consider that the 'spermatocytes' have (or had) a nutritive function. As yet there is no correlated change in the external sexual characters. This does not occur until the prawn is at least 22 months old (see p. 199). During the transition of the external characters the follicle cells return to the inter-breeding state, but as much as an eighth of the gonadial space may be occupied with the remaining spermatocytes. The latter gradually disappear and few prawns older than 25 months have any trace of male cells in the gonad. The oocytes completely fill the gonad, the largest having a maximum diameter of 0·18 mm. By the 27th month the growth rate of oocytes is maximum and their future development is similar to that of primary females of the same age. It was not appreciated until sections had been examined that there was a considerable lag in the change of male external characters. Thus typical male external characters may be present in a prawn 27 months old yet the ovary may show no remains of spermatocytes, no hypertrophy of the follicle cells and oocytes proliferating rapidly. There is no change in the male external characters and no proliferation of oocytes until the follicle cells (and perhaps the remaining spermatocytes) regress. It also appears (p. 203) that there is a similar correlation between the regression of the follicle cells and the development of the second batch of oocytes in the primary females. Inhibition by the follicle cells can be postulated. In case of the hermaphrodite female this may modify the effect of a sex reversal hormone of the X organ-sinus gland.

Secondary females. Gonadial evidence of sex change in immature prawns with male external characters were found. Earliest sections were of a 9½-month-old prawn with typical male external characters. In this case the oocytes were greatly developed and occupied two-thirds of the gonad. The peripheral oocytes were twice normal size for that age (0·09 mm max. diam.). Male cells were restricted to the inner lateral side and were atypical, the spermatocytes stained very densely and the nuclei were difficult to distinguish. Follicle cells were typical and were scattered among the spermatocytes as well as among the oocytes. A second prawn of the same age showing transitional external characters had no trace of male cells in the gonad. A third prawn, 11 months, showing transition characters, had male cells restricted to an eighth of the gonad. Others examined showed a similar picture. This clear lag between change in the gonad and change in the external characters will be further discussed (p. 215).

BREEDING

One brood is produced each year, and Rasmussen (1953) has shown that temperature affects the time of egg-laying and hatching. Thus, prawns from southern Norway (average temperature approximately 7° C) start to lay eggs about the second week in October and finish laying between early November and mid-December. Hatching occurs from the first week in March to the end of April (Fig. 9). There is an over-all period of 7 months when some females can be found with eggs attached to the pleopods. (The ovigerous period—completion of egg-laying to completion of hatching—is 5 months.)

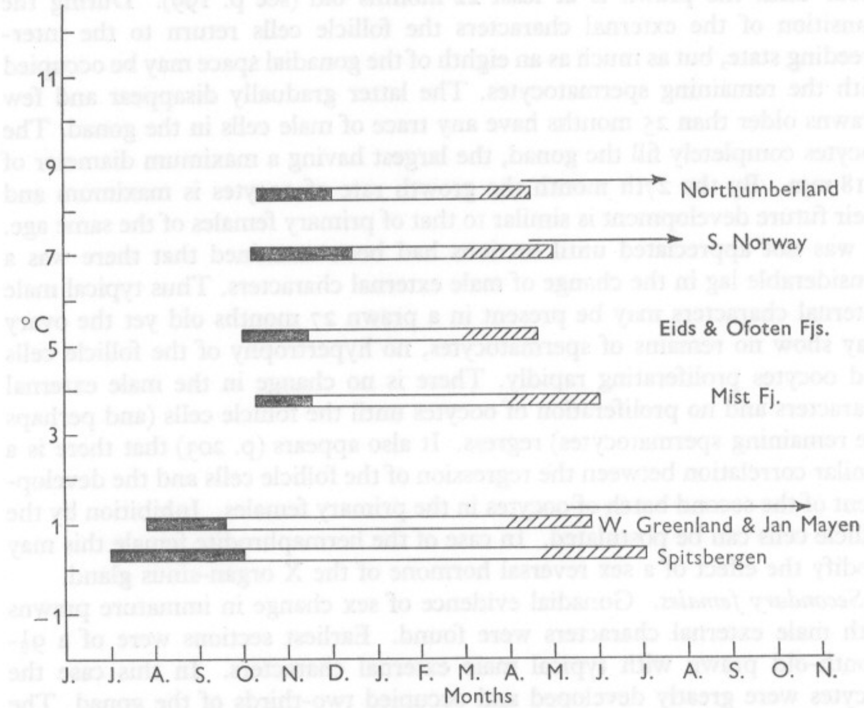

Fig. 9. Comparison of the breeding seasons of various prawn populations. Blacked section, egg-laying period; hatched section, period when larvae hatch. Arrows indicate duration of larval stages. Vertical arrangement corresponds to the mean temperature of the environment. Data extracted from Rasmussen (1953), Horsted & Smidt (1956) and the present work.

As temperature decreases so spawning starts earlier and hatching later. A maximum ovigerous period of 9 months is recorded for prawns of the Jan Mayen and Spitsbergen populations. It was expected that the Northumberland population with a high average temperature (8·5° C) would have a shorter ovigerous period. This was confirmed (Fig. 9 and Appendix II). Egg-laying commences about 10 October and all mature females are carrying eggs by 1 December. The larvae hatch between 10 March and 16 April. This represents an ovigerous period of about $4\frac{1}{2}$ months (2–4 weeks less than the southern Norwegian stocks). Hatching is completed about 2 weeks earlier and the larval stages may be expected to metamorphose at least this much earlier than the Norwegian stocks.

The number of eggs varies with the size of the prawn (Fig. 10). The Northumberland population shows significant differences from the southern Norwegian stocks. The minimum total length of an ovigerous Northumberland prawn is 80 mm compared with 85 mm of the Norwegian prawns. The maximum number of eggs carried by the Northumberland prawns rarely exceeds the minimum number of eggs carried by a Norwegian prawn of the same size (Fig. 10). Thus a Northumberland prawn 85 mm total length will carry an average of 160 eggs less than a Norwegian prawn of the same length,

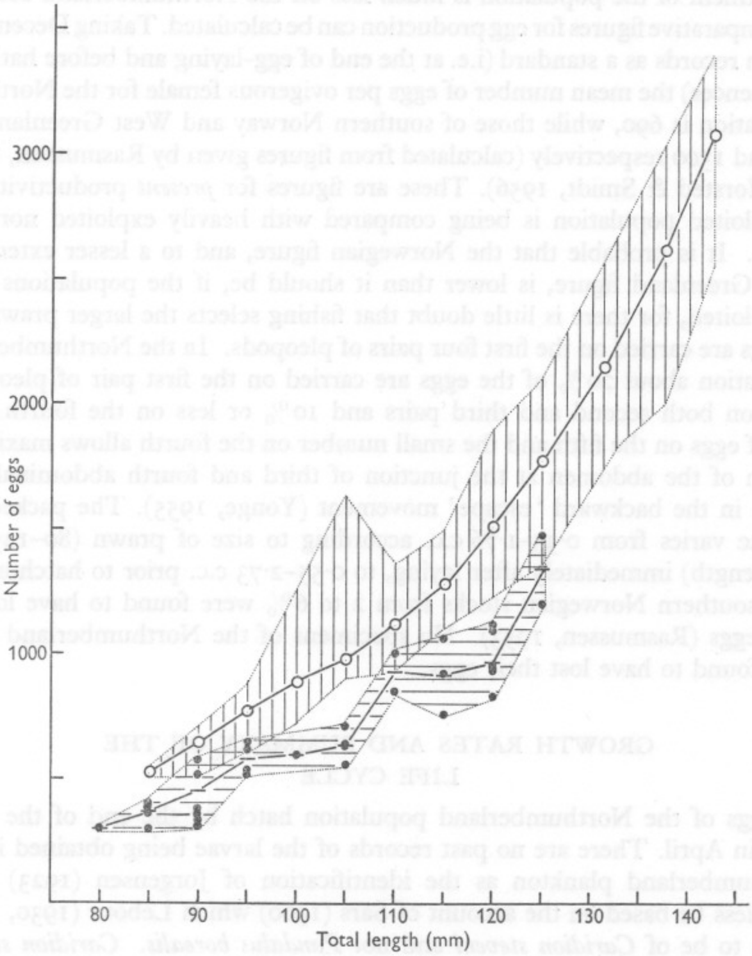

Fig. 10. Comparison of the numbers of eggs carried by *Pandalus borealis* of various lengths from Northumberland and Norwegian waters. Norwegian data (vertical hatching) extracted from Rasmussen (1953). Northumberland data (horizontal hatching). Mean numbers are indicated by the continuous line.

while the largest prawn (125 mm length) carries an average of 500 eggs less. The total number of eggs carried by the Northumberland prawn varies from 300 to 1500. Female prawns from Oslo Fjord may grow 20 mm longer than the largest Northumberland prawn and carry over 3000 eggs, i.e. the potential recruitment of the population is much less off the Northumberland coast.

Comparative figures for egg production can be calculated. Taking December–March records as a standard (i.e. at the end of egg-laying and before hatching commences) the mean number of eggs per ovigerous female for the North Sea population is 690, while those of southern Norway and West Greenland are 760 and 1300 respectively (calculated from figures given by Rasmussen, 1953; and Horsted & Smidt, 1956). These are figures for *present* productivity; an unexploited population is being compared with heavily exploited northern stocks. It is probable that the Norwegian figure, and to a lesser extent the West Greenland figure, is lower than it should be, if the populations were unexploited, for there is little doubt that fishing selects the larger prawn.

Eggs are carried on the first four pairs of pleopods. In the Northumberland population about 20% of the eggs are carried on the first pair of pleopods, 35% on both second and third pairs and 10% or less on the fourth. The lack of eggs on the fifth and the small number on the fourth allows maximum flexion of the abdomen at the junction of third and fourth abdominal segments in the backward 'escape' movement (Yonge, 1955). The packed egg volume varies from 0·35–1·76 c.c. according to size of prawn (80–125 mm total length) immediately after laying, to 0·55–2·73 c.c. prior to hatching.

In southern Norwegian stocks from 2 to 6% were found to have lost all their eggs (Rasmussen, 1953). No specimens of the Northumberland stock were found to have lost their eggs.

GROWTH RATES AND SUMMARY OF THE LIFE CYCLE

All eggs of the Northumberland population hatch by the end of the third week in April. There are no past records of the larvae being obtained in the Northumberland plankton as the identification of Jorgensen (1923) must doubtless be based on the account of Sars (1900) which Lebour (1930, 1940) shows to be of *Caridion steveni* and not *Pandalus borealis*. *Caridion steveni* occurs in Northumberland waters. Excellent descriptions of the larvae are given by Berkeley (1930). There are six stages during which time the larvae grow from 6 to 17 mm. Hjort & Ruud (1938) confirm this work from their plankton records from Oslo Fjord where metamorphosis occurs 3 months from hatching. First-stage larvae were collected from the Northumberland prawn grounds on 16 April 1957, but no other stages have been taken so far. Except for stages 1 and 2 both Berkeley and Hjort & Ruud found very few larvae in the plankton. Berkeley considers that they disappear from water close to the adult population at stage 3. Figures given by Hjort & Ruud (1938, p. 66) support this view.

The smallest post-larval prawn recorded by Hjort & Ruud (1938) was 21 mm total length (15 July 1933); but the average length of this brood on that date was 31 mm. This compares with 35 mm (2 August 1957) from Northumberland and 45 mm (October 1938) from Scottish waters (Ritchie) (Fig. 11, Appendix II). It has been established that the newly metamorphosed prawns tend to be in shallower water than the adults (Berkeley, 1930; Tåning, 1937; Hjort & Ruud, 1938; Horsted & Smidt, 1956) and these join the adult population some 9 or 10 months after hatching. In Oslo Fjord this joining of the two populations is marked by a heavy increase in the number of small prawns in catches during February–May representing between 88 and 97% of the total. Ritchie's records from Scottish waters (Appendix II) show a similar picture. There is a massive increase of young prawns in the Northumberland catches 7 months from hatching (Fig. 12). This early appearance of the new brood may be due to the small mesh size of the net, although a high growth rate and natant movement of the larvae under hydrographical conditions that tend to move them offshore may be of significance. An extensive programme of small-mesh trawling over the last 4 years in inshore waters (5–35 fathoms) has failed to catch any *P. borealis*. However, the present samples indicate that there is little mixing of the year groups, and perhaps even of sexes, for there are wide differences in the percentage composition of the various hauls (Figs. 11, 12). The young prawns of the new year-group may comprise from 20 to 80% of any sample. The average figure is 60% and this is maintained until the onset of egg-laying (Fig. 12).

Growth rate of the Northumberland population is given in Figs. 11 and 13. For the first 13 months the increased growth of the primary females over the males is slight and the average differences in total length at the end of the first year is approximately 2 mm. The average increase in length is high, 15–16 mm per month over this period. A slight drop in the rate from 7 to 8½ months coincides with low temperatures of the water during December and January before the spring increase of plankton but this may not be significant. After 13 months there is a considerable drop in the growth rate of the males which is probably related to increased testicular activity (p. 204). Between 13 and 23 months the average increase in length of the males is fairly constant at about 1·5 mm per month. There is no change at maturity. After 14 months the primary females also show a gradual falling off in their rate of growth until maturity is reached and the eggs are laid. At their first maturity the primary and secondary females are about 10 mm longer than the males. During the period when the eggs are carried (19–24 months) there is no growth, i.e. no moulting takes place while egg-bearing. From 23 to 28 months male external characters change to the female state. During this period growth rate is fairly rapid, approximately 4 mm/month. After the

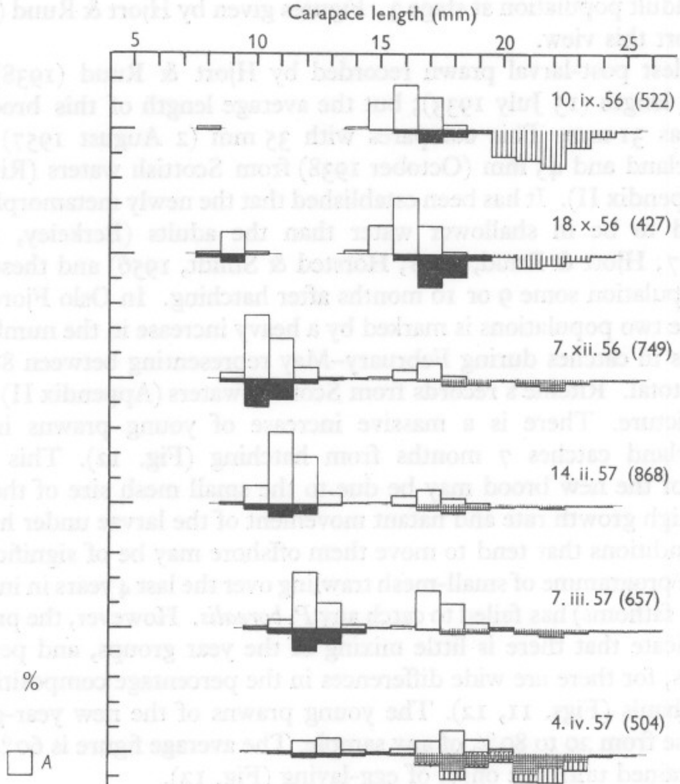

Fig. 11. Percentage size-composition of ten samples of *P. borealis* from Northumberland waters. *A*, males; *B*, immature females; *C*, females + eggs; *D*, females − eggs; *E*, transitional. The total number of prawns in each catch is given.

larvae have hatched the growth rate of the primary females is similar to the transitional males until 29 months, 2 months before the eggs are due to be laid. By this time the external characters have completely changed and the average length of a 29-month-old prawn is 108 mm. Further growth is slow and little more than 2 mm is added to the length before eggs are laid. After egg-laying no further growth occurs and the prawns die soon after the larvae hatch 4 or 5-months later. Ritchie's figures, which are a compilation of several years samples (Appendix II), show a similar picture.

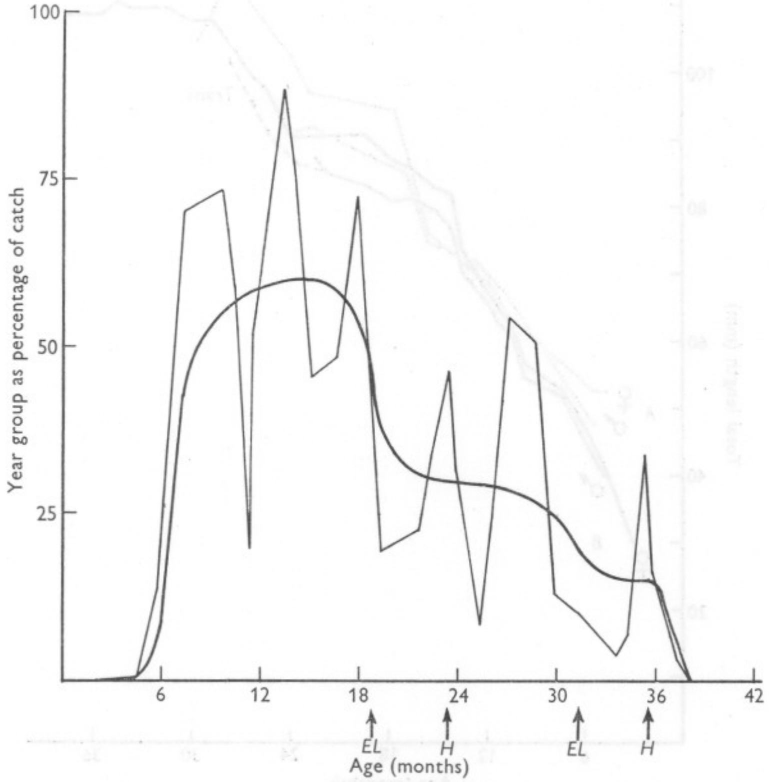

Fig. 12. Graph to show the variation in the percentage representation of one year group within the Northumberland population during the group's life. Estimated from the percentage composition of various samples. Thick line is the calculated mean. *EL*, egg-laying; *H*, hatching of larvae.

As might be expected, there is a very high mortality rate at the spawning period (Fig. 12). 50% of 18-month-old prawns die. This mortality takes place at egg-laying rather than egg-hatching and there is evidence of a second increase in the mortality rate at 31 months. Obviously this is of considerable significance for prawn fisheries, particularly as there is evidence that there is a tendency towards overfishing in Norwegian waters.

The growth rate of the Northumberland population (Fig. 14) is similar to that of southern Norway (Rasmussen, 1953). The higher temperature does not give rise to a marked increase in the growth rate. However, the maximum length attained by the Northumberland prawns (110 mm) is significantly less than that of other populations (> 120 mm). Although difficult to postulate a reason in the case of *P. borealis* this may well be a temperature effect. As a generalization, animals living at low temperatures are likely to be larger than related warm water species. It is of interest that the maximum prawn lengths of populations off the Scottish coast (Appendix II) are intermediate between Northumberland and southern Norway.

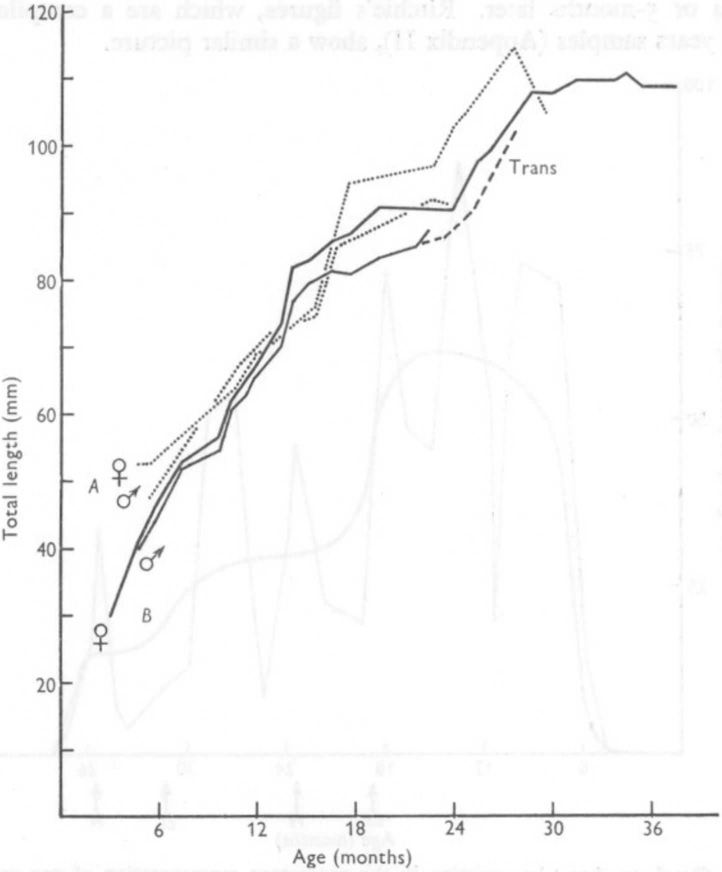

Fig. 13. Average growth-rate curves of male and female prawns from *A*, Scottish and *B*, Northumberland waters. *TRANS*, transitional Northumberland prawns.

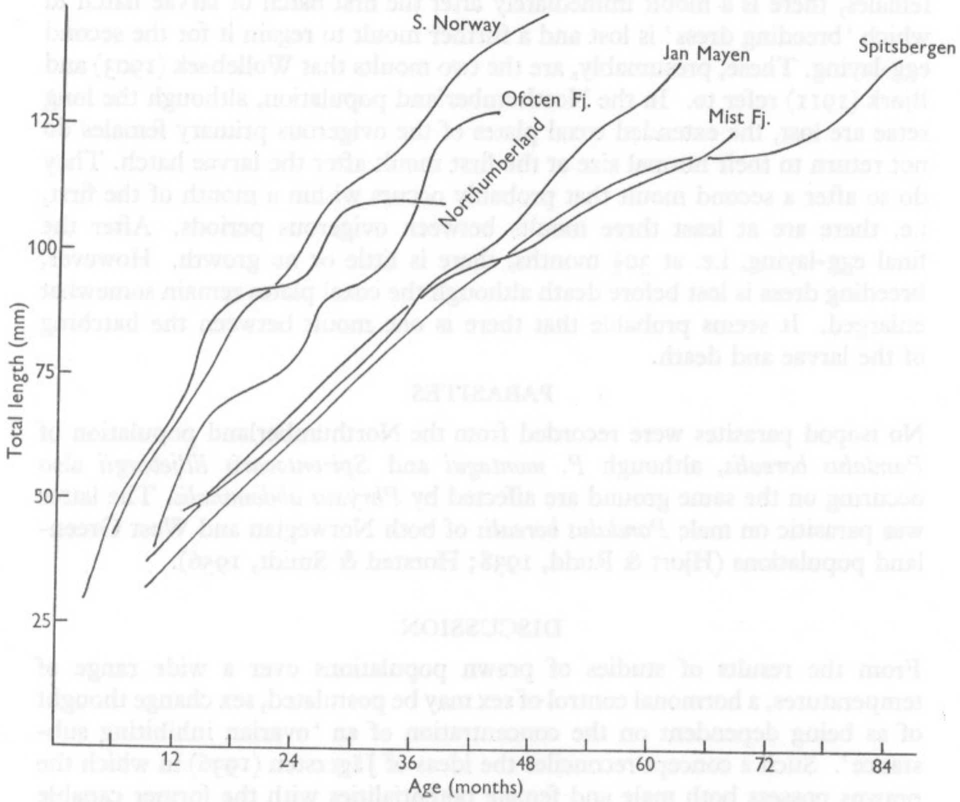

Fig. 14. Comparison of the growth rates of various prawn populations. Data from Rasmussen (1953) and present work.

MOULTS

Knowledge of the frequency of moults is incomplete. Berkeley (1930) shows that there are six larval stages. The seventh moult involves metamorphosis. Hjort & Ruud (1938) conclude that there are many moults during the first year of life until maturity, as many as fourteen in growing from 21 to 93 mm body length. Following maturity fewer moults take place. Wollebaek (1903) and Bjørk (1911) believe that large females have two moults only between each ovigerous period, although they note that 'soft' prawns are always present in their samples.

The present work gives additional information. There are at least three transitional first pleopod stages between full male and female structure. It is probable that four moults transform the male characters of the first pleopod and at least one more is required for final hypertrophy of appendix masculina. The assumption of 'breeding dress' involves a further moult. In the primary females, there is a moult immediately after the first batch of larvae hatch in which 'breeding dress' is lost and a further moult to regain it for the second egg-laying. These, presumably, are the two moults that Wollebaek (1903) and Bjørk (1911) refer to. In the Northumberland population, although the long setae are lost, the extended coxal plates of the ovigerous primary females do not return to their normal size at the first moult after the larvae hatch. They do so after a second moult that probably occurs within a month of the first, i.e. there are at least three moults between ovigerous periods. After the final egg-laying, i.e. at 30½ months, there is little or no growth. However, breeding dress is lost before death although the coxal plates remain somewhat enlarged. It seems probable that there is one moult between the hatching of the larvae and death.

PARASITES

No isopod parasites were recorded from the Northumberland population of *Pandalus borealis*, although *P. montagui* and *Spirontocaris lilljeborgii* also occuring on the same ground are affected by *Phryxus abdominalis*. The latter was parasitic on male *Pandalus borealis* of both Norwegian and West Greenland populations (Hjort & Rudd, 1938; Horsted & Smidt, 1956).

DISCUSSION

From the results of studies of prawn populations over a wide range of temperatures, a hormonal control of sex may be postulated, sex change thought of as being dependent on the concentration of an 'ovarian inhibiting substance'. Such a concept reconciles the ideas of Jägersten (1936) in which the prawns possess both male and female potentialities with the former capable of repression early in life, and of Hjort & Ruud (1938) who postulate a 'labile equilibrium' between male and female potentialities, with that of Rasmussen (1953) who links sex with size. Recently Carlisle is reported to have found that sex reversal in *P. borealis* is essentially similar to that in *Lysmata seticaudata* (*Rep. of Council of M.B.A.* 1956–7, p. 17)—'reversal is controlled primarily by action of the X organ-sinus gland complex in secreting the ovarian inhibiting substance, which appears to be the only hormone concerned. This hormone, or rather the cessation of its secretion, is responsible for the control of the onset of sex reversal. *The actual assumption of female form seems to take place at the moult following the attainment of minimum ovarian size. The degeneration of the testis which follows sex reversal* is probably to be attributed to the blocking of the opening of the vasa deferentia which *takes place when the animal develops a female shell*'.[1] While this report may fit the observed details of the biology of the Swedish prawns on which this work was based, it does not entirely fit with the present work on the Northumberland population. Although there seems little doubt that the control of the

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[1] Author's italics.

attainment of the female phase is due to lack of hormonal secretion of the X organ-sinus gland complex, it is clear that 'minimum ovarian size' is not critical, at least in southern Norway and North Sea populations. Presumably temperature must play a considerable role in sex reversal. In addition, the present study shows that testis degeneration begins before the animal develops a female shell. External changes may lag considerably behind gonadal changes and specimens found with no trace of spermatocytes may still show male external characters. Sections suggest that the state of the follicular tissue may be of importance in the change of external characters. Until the follicular tissue degenerates there is no external change. Follicular tissue is not proliferated in immature specimens so that there is no bar to the rapid change of external form. Sections also suggest that proliferated follicular tissue has an important role during the incubation of the eggs perhaps as a growth inhibitor to the prawn and the onset of the increase in the rate of proliferation of oocytes also appears to coincide with degeneration of follicular tissue.

While the X organ-sinus gland is probably all important, modification of its action may come through hormones produced within the gonad. If growth rate and gonadal development are controlled directly or indirectly by hormones, it is likely that maturity will be reached within narrow size limits, and temperature, by its general effect on metabolism (including hormone action) will influence the age of maturity and also the onset of the breeding season.

Gonadal development and histology is similar to other *Pandalus* species described by Berkeley (1930), Aoto (1952) and Mistakidis (1957).

Present data show that there can be little prospect of a fishery for this prawn in the North Sea. Ritchie's samples from Scottish waters (mostly from the Fladen area) show that the population is patchy and that numbers are not very large. The *maximum* catch off the Northumberland coast was 3 l./h using a 9 ft. beam trawl. Presumably this can be increased by using a larger trawl but cannot compare with the catches, considered very good, of 60–100 l./h from the Gulf of Maine and Norwegian waters. Even higher catches are recorded from West Greenland (Horsted & Smidt, 1957). It is difficult to extract figures from the papers referred to, but the average daily yield per boat in Norwegian waters, approximately 10 kg ≡ 18 l., could perhaps be equalled off Northumberland only under the most favourable conditions. This is likely to be the exception rather than the rule.

The ground is not extensive and is some distance from the coast. By using the commercial pink shrimp trawl, large numbers of small prawns were caught during this work and if normal British shrimp trawls were used to fish the stock it would soon be depleted. Stocks will survive if only the largest prawns (>95 mm) are removed, fishing being limited to the period May to September when recently hatched prawns have yet to join the adult stocks.

Weather largely limits the use of small inshore boats to this period anyway, but it must be concluded that this population can only support an occasional fishery.

SUMMARY

Data on the distribution of *Pandalus borealis* have been brought up to date, and the factors controlling its distribution (temperature, salinity, substratum and depth) are discussed.

An account of the biology of the population off the Northumberland coast is given and compared with accounts of work on other populations. Knowledge of the biology of this species now extends over the entire north-south range in the eastern Atlantic.

Details of the histology and development of the gonads are given, particularly with respect to the development of the ova and to sex reversal. Sex changes in the gonad are considered in relation to changes in external form.

The growth rate of the North Sea prawn is described and compared with that of other populations.

It is unlikely that the North Sea populations can provide an additional fishery.

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APPENDIX I

Records of Pandalus borealis *from British Waters*

	Date	Position	Depth (m)	No. of specimens
J. A. Grieg	1904	57° 9′ N.–1° 30′ W.	96	?
R. A. Todd	26. viii. 07	55° 31½′ N–0° 33′ W.	90	30
H. Wedemeyer	1912	54° 24′ N–2° 59′ E	40	1
H. O. Bull	8. ii. 33	12 miles E. of Coquet	?	6
	28. viiii. 33	Off Coquet	?	Hundreds
	27. i. 34	'N.E. Bank'	?	1
	30. i. 34	Off Coquet	?	3
	10. iii. 34	Off Coquet	?	1
	20. ix. 34	17 miles E. of Tyne	?	Hundreds
	29. i. 35	Off Newbiggin	?	3
	10. ii. 35	Off Newbiggin	?	3
	24. ix. 35	14 miles E.S.E. Tyne	?	Many
A. Ritchie	7. iv. 36	58° 05′ N.–0° 31′ E.	150–152	81
	8. iv. 46	58° 27′ N.–0° 01′ W.	145–147	59
	26. iv. 36	58° 30′ N.–0° 24′ W.	140	1
	7. iv. 36	58° 05′ N.–0° 05′ W.	128–133	1
	13. viii. 36	58° 07′ N.–0° 52′ E.	150	114
	13. viii. 36	58° 32′ N.–0° 56′ E.	140	32
	19. ix. 36	58° 21′ N.–0° 04′ W.	134	6
	9. iii. 37	58° 05′ N.–0° 31′ E.	149	170
	24. iii. 37	58° 05′ N.–0° 25′ W.	135	16
	17. viii. 37	58° 02′ N.–0° 30′ E.	145	51
	24. iii. 38	58° 05′ N.–0° 05′ W.	140	26
	2. v. 38	57° 47′ N.–0° 40′ E.	127	48
	14. v. 38	60° 06′ N.–0° 10′ E.	121	8
	9. v. 38	58° 50′ N.–0° 26′ E.	145	6
	9. x. 38	55° 32′ N.–0° 55′ W.	98	196
	16. iii. 39	58° 01′ N.–0° 31′ E.	145	104
	18. ii. 39	59° 01′ N.–0° 25′ E.	140	12
	26. iv. 39	58° 05′ N.–0° 05′ W.	147	156
	13. iv. 39	57° 47′ N.–0° 40′ E.	130	2
	23. viiii. 39	58° 55′ N.–0° 25′ W.	132	18
J. A. Allen	1955–58	13 miles E. of Blyth	90	Hundreds
British Museum (Nat. Hist.)	6. xi. 07	55° 31½′ N.–0° 53′ W.	100	12
	16. x. 35	14 miles E.S.E. Tyne	80	10

APPENDIX II

Scottish samples 1936–39

Collected by Dr A. Ritchie, Scottish Home Department Laboratory, Aberdeen.

(Young prawns, classed as 'immature' by Dr Ritchie, have been assumed to be immature females on the grounds that (i) males of a similar size range are recorded from the same samples, and (2) the present work shows that young prawns of the same size from Northumberland can be sexed.)

Total length (mm)	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total	♂	Trans	Immature ♀	♀+Eggs	♀−Eggs	Total
45	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	1	—	—	2
50	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1	4	—	1	—	—	5
55	13	—	—	—	—	13	—	3	1	—	—	4	1	—	1	—	—	2	—	—	—	—	—	—	1	—	—	—	—	1	7	—	—	—	—	7
60	20	—	2	—	—	22	14	4	5	—	—	23	8	—	5	—	—	13	—	—	—	—	—	—	—	—	—	—	—	—	1	—	—	—	—	1
65	36	—	4	—	—	40	26	4	13	—	—	43	16	—	1	—	—	17	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
70	16	—	5	—	—	21	20	3	8	—	—	31	13	—	5	—	—	18	2	—	1	—	—	3	—	—	—	—	—	—	—	—	—	—	—	—
75	3	1	1	1	—	6	8	3	1	—	—	12	6	—	1	—	—	7	14	—	3	—	—	17	—	—	—	—	—	—	2	—	—	—	—	2
80	2	—	—	3	—	5	1	—	—	—	—	1	2	—	—	—	—	2	27	—	8	—	—	35	—	—	—	—	—	—	9	—	—	—	—	9
85	8	7	—	10	—	25	3	2	—	—	1	6	—	—	—	—	—	—	35	1	13	—	—	49	1	—	—	—	—	1	35	—	—	—	6	41
90	19	19	—	14	1	53	13	8	—	—	3	24	—	—	—	—	—	—	15	—	11	—	—	26	—	—	—	—	—	—	15	—	—	—	25	40
95	19	35	—	4	—	58	7	22	—	—	5	34	—	—	—	—	1	1	5	2	4	—	4	15	—	—	—	—	1	1	2	—	—	—	29	31
100	4	14	—	11	1	30	—	48	—	—	20	68	—	—	—	—	—	—	1	4	—	—	15	20	—	—	—	—	1	1	1	—	—	—	26	27
105	2	13	—	13	1	29	—	17	—	—	11	27	—	—	—	—	1	1	5	—	—	—	17	22	—	—	—	—	1	1	1	—	—	1	13	15
110	—	9	—	8	2	19	—	17	—	1	4	22	—	—	—	—	—	—	—	—	—	—	8	8	—	—	—	—	—	—	—	—	—	—	11	11
115	—	2	—	2	1	5	—	—	—	—	4	4	—	—	—	—	1	1	—	—	—	—	11	11	—	—	—	—	—	—	—	—	—	—	4	4
120	—	—	—	—	1	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	8	8	—	—	—	—	—	—	—	—	—	—	1	1
125	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
130	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
135	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
140	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T	142	100	12	66	8	328	92	131	28	1	49	301	46	—	13	—	3	62	105	7	40	—	63	215	3	—	—	—	3	6	78	—	2	1	118	196
Date	March 1937 ’38 ’39						April 1936 ’39						May 1939						August 1936 ’37 ’39						September 1936						October 1938					

APPENDIX II

Northumberland samples, 1956–57

Carapace length (mm)	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total
6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8	1	—	2	—	—	3	6	—	2	—	—	8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9	—	—	—	—	—	—	35	—	12	—	—	47	21	—	11	—	—	32	3	—	4	—	—	7	—	—	—	—	—	—
10	—	—	—	—	—	—	3	—	2	—	—	5	178	—	79	—	—	257	61	—	26	—	—	87	5	—	1	—	—	6
11	—	—	—	—	—	—	—	—	—	—	—	—	121	—	63	—	—	184	228	—	72	—	—	300	22	—	15	—	—	37
12	—	—	—	—	—	—	—	—	—	—	—	—	33	—	15	—	—	48	160	—	39	—	—	199	148	—	66	—	—	214
13	—	—	—	—	—	—	—	—	—	—	—	—	2	—	1	—	—	3	36	—	5	—	—	41	65	—	42	—	—	107
14	2	—	—	—	—	2	6	—	—	—	—	6	1	—	—	—	—	1	2	—	1	—	—	3	10	—	14	—	—	24
15	29	—	2	—	—	31	47	—	—	—	—	47	5	—	—	—	—	5	4	—	—	—	—	4	1	—	—	—	—	1
16	92	—	9	—	—	101	93	—	12	—	—	105	29	—	—	2	—	31	29	—	—	3	—	32	7	—	—	—	—	7
17	63	—	28	—	—	91	50	—	58	—	—	108	51	—	—	6	—	57	53	—	—	15	—	68	92	—	—	10	—	102
18	7	—	16	—	—	23	4	—	30	—	—	34	10	—	—	22	—	32	24	—	—	37	—	61	66	—	—	15	—	81
19	—	—	4	—	5	9	—	—	10	—	—	10	—	—	—	18	—	18	1	—	—	18	—	19	18	—	—	10	—	28
20	1	—	—	—	61	62	—	—	1	—	2	3	—	—	—	6	—	6	—	—	—	14	—	14	2	—	—	3	—	5
21	—	—	—	—	65	65	—	—	—	—	24	24	—	—	—	21	—	21	—	—	—	11	—	11	—	—	—	13	—	13
22	—	—	—	—	81	81	—	—	—	—	20	20	—	—	—	34	—	34	—	—	—	16	—	16	—	—	—	19	—	19
23	—	—	—	—	39	39	—	—	—	—	9	9	—	—	—	13	—	13	—	—	—	3	—	3	—	—	—	8	—	8
24	—	—	—	—	13	13	—	—	—	—	1	1	—	—	—	5	—	5	—	—	—	3	—	3	—	—	—	2	—	2
25	—	—	—	—	3	3	—	—	—	—	—	—	—	—	—	2	—	2	—	—	—		—	—	—	—	—	2	—	2
26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—		—	—	—	—	—	1	—	1
T	195	—	61	—	266	522	244	—	127	—	56	427	541	—	169	129	—	749	601	—	147	120	—	868	436	—	138	83	—	657
Date	10 September 1956						18 October 1956						7 December 1956						14 February 1957						7 March 1957					

Carapace length (mm)	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total	♂	Trans	Immature ♀	♀ + Eggs	♀ − Eggs	Total
6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
7	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
8	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
9	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
10	2	—	—	—	—	2	—	—	2	—	—	2	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
11	2	—	3	—	—	5	2	—	4	—	—	6	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
12	25	—	11	—	—	36	49	—	20	—	—	69	1	—	—	—	—	1	—	—	—	—	—	—	—	—	—	—	—	—
13	30	—	10	—	—	41	165	—	58	—	—	223	22	—	1	—	—	23	3	—	—	—	—	3	—	—	—	—	—	—
14	7	—	8	—	—	15	52	—	33	—	—	85	50	—	25	—	—	75	36	—	5	—	—	41	4	—	1	—	—	5
15	1	—	1	—	—	2	12	—	12	—	—	24	17	—	25	—	—	42	169	—	29	—	—	198	53	—	16	—	—	69
16	9	—	—	1	1	11	7	—	1	1	3	12	4	—	14	—	—	18	176	—	58	—	—	234	90	—	44	—	—	134
17	25	—	—	17	8	50	23	3	—	1	11	38	—	—	3	—	—	3	30	—	39	—	—	69	25	—	42	—	—	67
18	46	—	—	37	17	100	73	7	—	2	24	106	—	1	—	—	1	2	3	3	8	—	7	21	7	6	11	—	11	35
19	27	1	—	26	3	57	40	19	—	1	24	84	—	—	—	—	5	5	—	6	—	—	29	35	—	20	—	—	39	59
20	5	4	—	13	5	27	7	4	—	—	12	23	—	—	—	—	6	6	—	21	—	—	63	84	—	13	—	—	119	132
21	—	—	—	41	17	58	—	—	—	4	42	46	—	—	—	—	3	3	—	9	—	—	28	37	—	2	—	—	83	85
22	—	—	—	30	30	60	—	—	—	4	50	54	—	—	—	—	5	5	—	—	—	—	9	9	—	—	—	—	30	30
23	—	—	—	18	17	35	—	—	—	—	15	15	—	—	—	—	—	—	—	—	—	—	4	4	—	—	—	—	23	23
24	—	—	—	4	1	5	—	—	—	—	7	7	—	—	—	—	—	—	—	—	—	—	1	1	—	—	—	—	4	4
25	—	—	—	—	1	1	—	—	—	—	1	1	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	4	4
26	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—	—
T	179	5	33	187	100	504	430	33	130	13	189	795	94	1	68	—	20	183	417	39	139	—	141	736	179	41	114	—	313	647
Date	4 April 1957						16 April 1957						7 June 1957						2 July 1957						2 August 1957					