

NOTES ON THE GROWTH AND BIOLOGY OF THE PRAWN *PANDALUS BONNIERI* CAULLERY

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(Text-figs. 1 and 2)

Pandalus bonnierii Caullery has for a long time been known to occur in considerable numbers in the deeper waters of the Clyde Sea Area. Its life history and growth have been investigated, with special reference to sexual development, since the genus *Pandalus* contains not only species that are dioecious, but also those that are protandrous.

The author expresses indebtedness to the skipper and crew of M.V. *Calanus* for their unfailing help in collecting the material, and to Miss E. R. Wallace for assistance in measuring specimens. Thanks are also due to Dr A. Ritchie at the Fisheries Laboratory, Aberdeen, for supplying records of the occurrence of *P. bonnierii* on the west coast of Scotland and in the North Sea, and to colleagues at the Marine Station for assistance in preparing this paper.

COLLECTION OF MATERIAL AND DATA

All adult prawns were caught in the Firth of Clyde on trawling grounds off the Island of Bute (National Grid Reference 26/1159-1162) at a depth of 70-90 m. The gear used was an 8 ft. Agassiz trawl having a net mesh of $\frac{1}{2}$ in. bar, which was found to retain prawns above 7 mm. carapace length (3.7 cm. total length). The duration of a haul was 15 min., and such hauls were repeated until a sufficient number of specimens had been obtained for the day's sample.

For catching prawns smaller than 7 mm. carapace length, a 2 m. stramin net was fixed to a small beam trawl, so modified that the net worked about 6 in. above the muddy bottom. Early post-larval stages were seldom obtained in any numbers.

All specimens above 5 mm. carapace length were measured with fine calipers in the fresh condition and then fixed in 10% formalin for subsequent preservation in 70% alcohol.

The standard measurement made was the 'length of the carapace', being the distance from the posterior margin of the eye socket to the dorsal posterior

margin of the carapace. Measurement was made to the nearest 1 mm. below, and the data were recorded in 1 mm. groups.

An approximation to the *total* length, including the rostrum, can be obtained by multiplying the *carapace* length in the male by 5.2, and in the female and juvenile by 5.4. In both males and females of carapace length exceeding 17 mm., however, the total length calculated in this manner works out on the high side.

GEOGRAPHICAL DISTRIBUTION

P. bonnieri Caullery is essentially a deep-water prawn and, like *P. borealis* Krøyer, is usually found at a depth of about 100 m. Its distribution extends from Iceland (Stephensen, 1939, p. 22) to the Bay of Biscay (Caullery, 1896). It does not appear to be very plentiful round Iceland or to enter Greenland waters. From Norway it is recorded by Wollebaek (1908) from several localities in both the south and west. Dr Ritchie has kindly supplied me with sixty records of its occurrence in the North Sea and from the west coast of Scotland. These records show that it is taken frequently in the North Sea from the Shetland Isles to Peterhead, and on one occasion was taken as far south as $56^{\circ} 03' N.$, $1^{\circ} 45' W.$ The majority of specimens were obtained beyond the 100 m. line along the western edge of the deep central basin of the North Sea, but they were not abundant at any locality. On the west coast of Scotland it is also taken beyond the 100 m. line and appears to be generally distributed, the greatest numbers being obtained off the Butt of Lewis and south of South Uist. In general, records are absent for the north of Scotland and west of the Outer Hebrides, but the prawn has been obtained on two occasions west of the Orkneys. Dr Ritchie suggests that their absence from these areas may be due to the texture of the sea-floor in those localities. Calman (1899) was the first to record it from the Firth of Clyde. He also records it from the west coast of Ireland and off Rockall. Kemp (1910) states that it is abundant in the Irish Sea and off the west coast of Ireland, but it has not so far been taken off the south of Ireland. It is not recorded in the *Marine Fauna of the Isle of Man* (Moore, 1937), but Mr N. S. Jones of the Marine Biological Station, Port Erin, informs me that he has taken it frequently since 1946 on muddy bottom in 90-130 m., 7-11 miles north-west of Bradda Head. It does not appear in the *Plymouth Marine Fauna* (Mar. Biol. Assoc., 1931). Lebour (1940), however, records the larvae as occurring in plankton off Seven Stones Lightship, Scilly Isles ($50^{\circ} 03\frac{1}{2}' N.$, $6^{\circ} 04\frac{1}{2}' W.$).

OCCURRENCE IN THE CLYDE

In the Clyde *P. bonnieri* is taken frequently in water as shallow as 40 m., although it is most abundant at depths of 90-130 m., on grounds composed of soft grey mud, inhabited by an animal community similar to that associated with *P. borealis* as described by Hjort & Ruud (1938).

The commonest bivalve molluscs are *Abra alba* (Wood) and various species of *Nucula*, of which *N. nucleus* (L.) and *N. sulcata* Bronn are the commonest. *Thyasira flexuosa* (Montagu) is, however, rare and *Chlamys septemradiata* (Müller) is not very abundant on this ground. Among the annelids, *Pectinaria belgica* (Pallas), *Lipobranchius jeffreysii* (McIntosh) and *Glycera rouxi* Audouin & M.-Edwards are all very plentiful. Of the Crustacea, *Spirontocaris spinus* var. *lilljeborgi* (Danielssen), *Crangon allmani* Kinahan and *Nephrops norvegicus* L. are the commonest species.

MIGRATION

Berkeley (1931) drew attention to evidence that larvae of pandalids metamorphose in shallow water, and Poulsen (1946) also found young *Pandalus borealis* in shallow water round Denmark. In the Clyde the normal prawn grounds, and the shallow water areas in the neighbourhood, were trawled with a bottom stramin net (see collection of material and data) during June and July 1951 for early metamorphosed prawns. These were not obtained in any numbers until 31 July at a depth of 130 m. No information was therefore obtained on the movements of young *P. bonnieri*.

Adult prawns could not be found during August and September 1951 in the Clyde. According to Hjort & Ruud (1938) *P. borealis* rises off the bottom during dull weather and during the hours of darkness. A similar habit in *P. bonnieri* might account for the difference in numbers on successive days, but not for the scarcity of specimens during two months. It is possible that both the young and adults moved into the nearby inshore boulder-strewn grounds where trawling was impossible.

BREEDING

In the Clyde the ovaries of adult prawns begin to mature in July, when they show through the carapace as a greenish mass. In September the fully ripe ovaries darken to a deep sage green. Egg-laying begins at the end of October with the larger size-groups laying first (Fig. 1A), and continues for about 6-8 weeks. By the end of December the whole adult female population is in berry (Fig. 1B).

The eggs when first laid are a beautiful deep green colour and oval in shape (c. 2×1.5 mm.). The sage-green colour of the newly laid egg in *P. bonnieri* is in contrast with the blue-green egg of *P. borealis*, the light emerald green of *P. montagui* Leach and the fawn colour in *P. propinquus* G. O. Sars.

The green colour gradually disappears as the larvae develop, and just before hatching takes place the green is almost replaced by pale violet and yellow pigmentation with the prominent red chromatophores of the thoracic region clearly showing. The eye pigmentation develops gradually and is first seen after about 3 months' incubation.

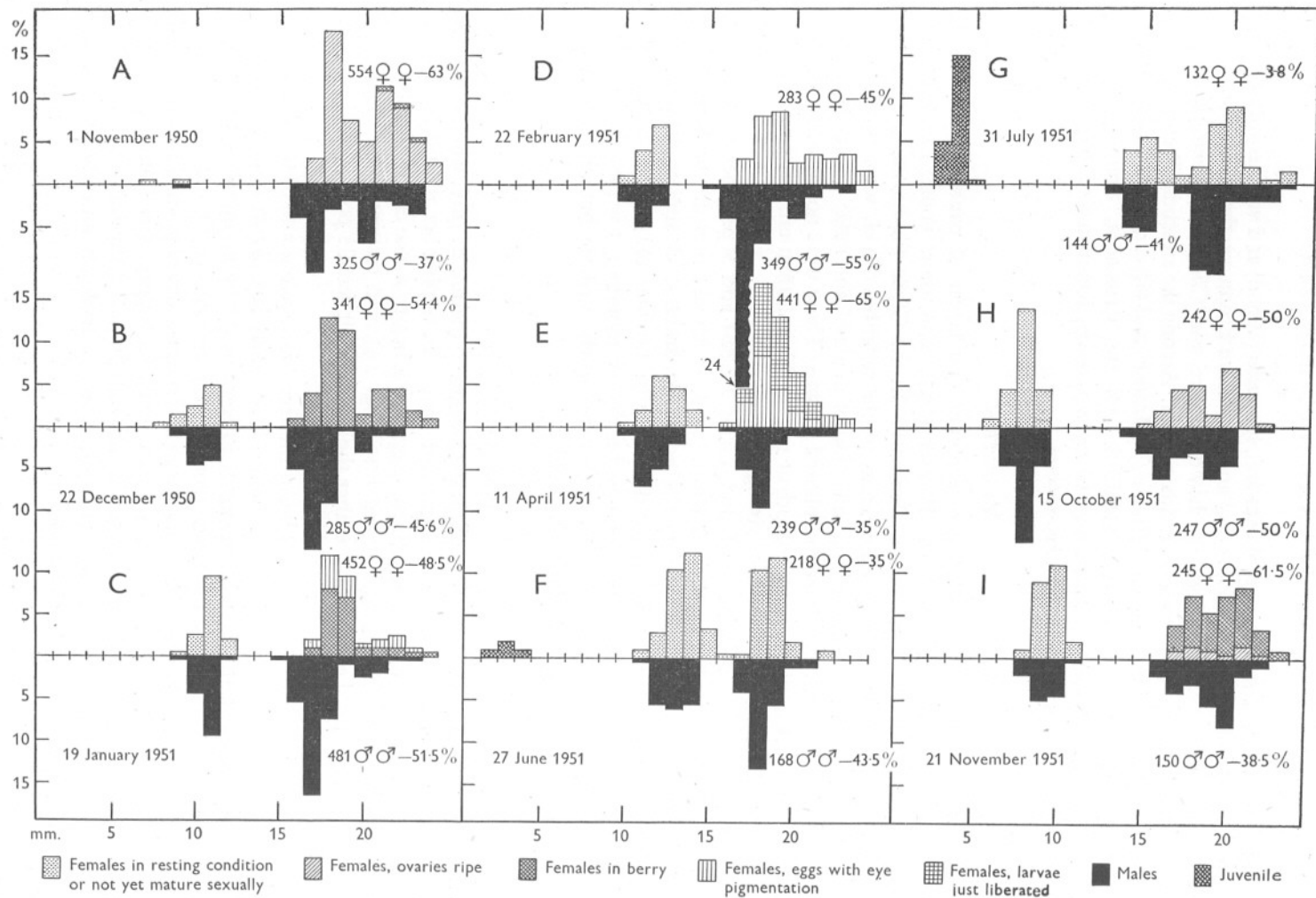


Fig. 1.

The number of eggs laid by *P. bonnieri* increases from approximately 1000 at 16 mm. carapace length to 4000 at 24 mm. carapace length. Within any given millimetre size-group the variation appears to be $c. \pm 10\%$.

In 1951 the first larvae were liberated in the third week in February, although the number of prawns that had completed incubation was too small to be recorded on the graph for 22 February (Fig. 1D). The total hatching period extended over 2 months and all the larvae were liberated by the end of April (Table I).

It is probable that moulting and the loss of the ovigerous setae take place within 10 days of the liberation of the larvae from the eggs, but the period is not known. Höglund (1943) has described and illustrated the ovigerous setae for *P. borealis* and shown the arrangement to be similar for *P. bonnieri*.

TABLE I. BREEDING CONDITION IN SECOND- AND THIRD-YEAR
PANDALUS BONNIERI

Date (1950-1)	Ovary ripe (%)	Eggs (%)	Eggs with eye pigmentation (%)	Larvae liberated (%)
15 Oct.	100	—	—	—
26 Nov.	22	78	—	—
6 Dec.	3	97	—	—
19 Jan.	—	60	40	—
22 Feb.	—	—	98	2
19 Mar.	—	—	90	10
11 Apr.	—	—	54	46
5 May	—	—	—	100

SEXUAL DIFFERENTIATION IN *PANDALUS BONNIERI*

Over one whole year, the percentage of males in the catches has varied between 35 and 55%, about a mean of 45%, and that of the females between 38 and 65%, about a mean of 55%. The sex was determined by the examination of the pleopods under the binocular microscope. The sex characters of *P. bonnieri* agree very closely with those given by Wollebaek (1908) for *P. borealis*. Among the males no transitional form of pleopod corresponding to that illustrated by Jägersten (1936) for *P. borealis* was found.

Many male prawns were dissected, but not one was found to possess oviducts as well as vasa deferentia. Sections of the male gonad in prawns aged 18-30 months have been prepared, from which it could be seen that the gonad

Legend to Fig. 1.

Fig. 1. The percentage size distribution of *Pandalus bonnieri* in the Clyde Sea Area during 1950-51. Females above and males below the zero line. To the left the date of collection. To the right the number of females and males measured in each sample in total and in percentage of the whole sample. The juvenile population in Fig. 1 is included in the total percentage although captured with a different gear (see p. 259). In the females the state of sexual maturity is also shown.

was composed entirely of testicular tissue with no trace of ovarian tissue such as was found by Jägersten in *P. borealis*.

I therefore think *P. bonnieri* is completely dioecious. This finding is confirmed by Dr Ritchie in a personal communication.

RATE OF GROWTH IN *PANDALUS BONNIERI*

The data obtained on growth are shown in graphic form in Figs. 1 and 2 and summarized in Table II.

In preparing Fig. 2 the graph relates to modal lengths and not to arithmetic means as were used by Hjort & Ruud (1938) for *P. borealis*, by Höglund (1943) for *Leander squilla* (L.) and by Forster (1951, *a, b*) for both *L. squilla* and *L. serratus* Pennant.

TABLE II. GROWTH OF *PANDALUS BONNIERI*

Month of year	O-Group		I-Group		II-Group	
	Age in months	Carapace length (mm.)	Age in months	Carapace length (mm.)	Age in months	Carapace length (mm.)
Apr.	0-2	0.9-1.2	12-14	♂ 11-12 ♀ 12	24-26	♂ 18 ♀ 18-19
June	2-4	2.5-3.0	14-16	♂ 12-14 ♀ 13-14	26-28	♂ 18 ♀ 18-19
July	3-5	3-5	15-17	♂ 14-15 ♀ 15	27-29	♂ 18-19 ♀ 19-20
Oct.	6-8	♂♀ 7-9	18-20	♂ 16 ♀ 17-18	30-32	♂ 19 ♀ 20
Nov.	7-9	♂♀ 9-10	19-21	♂ 17 ♀ 18	31-33	♂ 20 ♀ 21-22
Dec.	8-10	♂♀ 10-11	20-22	♂ 17 ♀ 18-19	32-34	♂ 20 ♀ 21-22
Jan.	9-11	♂♀ 10-11	21-23	♂ 17 ♀ 18-19	33-35	♂ 20 ♀ 22
Feb.	10-12	♂ 11 ♀ 12	22-24	♂ 17 ♀ 18-19	34-36	♂ 20 ♀ 21

On hatching in March and April the larvae have a carapace length of 0.9 mm. (total length 4.2 mm.), and by the end of June, now from 2 to 4 months old, they have metamorphosed and have a carapace length of 2.5-3 mm. Metamorphosis takes place at about 2.2 mm. carapace length. By the end of July they have increased their carapace length from 3 to 5 mm., and are still juvenile, with the sexes undifferentiated. At 5 mm. carapace length it becomes possible to distinguish the sexes by the shape of the pleopods, but the developing males at this early stage are less readily

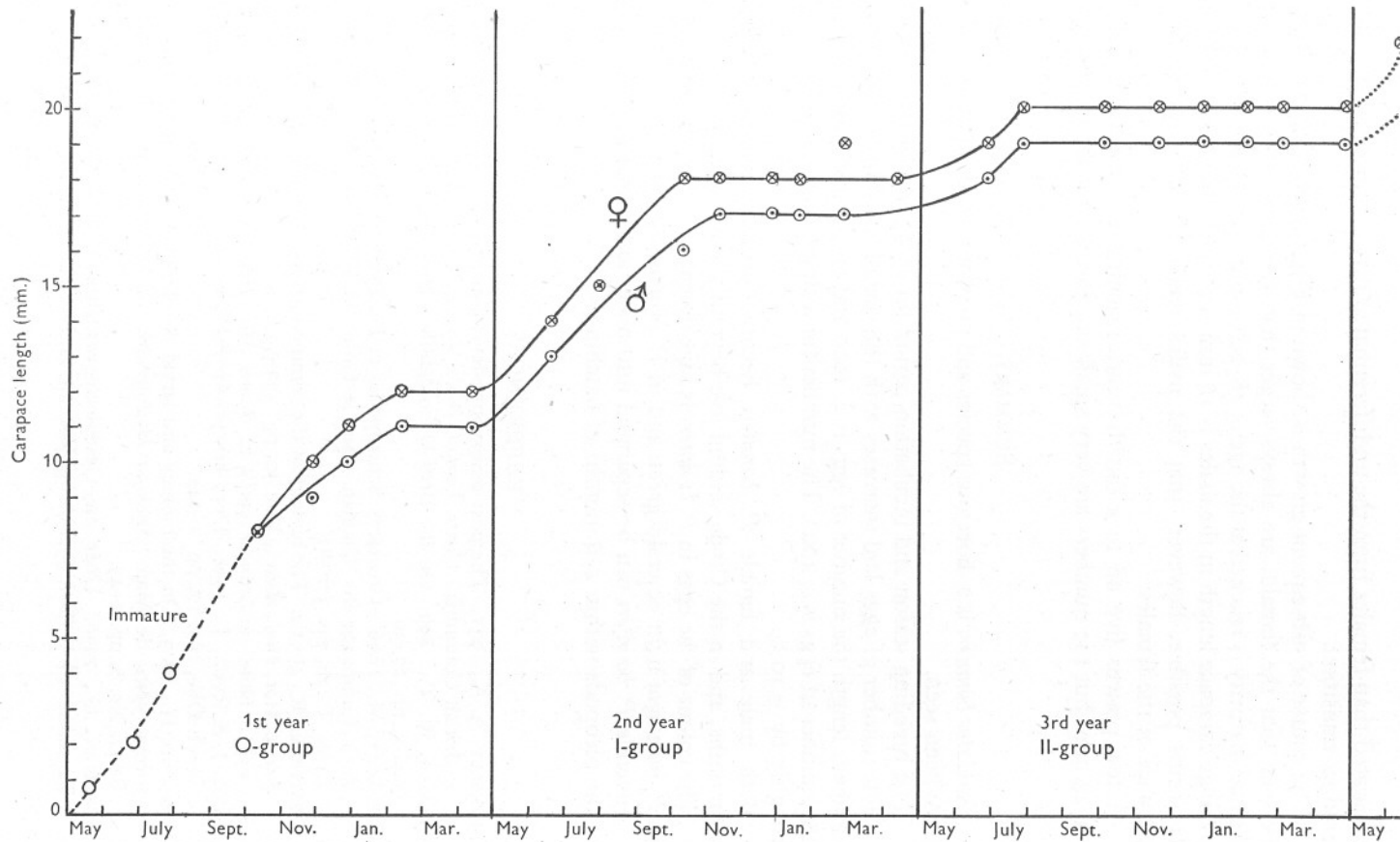


Fig. 2. *Pandalus bonnierii*. Modal lengths of various samples of three year-groups, forming an approximate growth curve.

separated than females from the undifferentiated juveniles because of a more gradual transition.

The course of subsequent growth is shown in Fig. 2 and Table II. It will be seen that the females are always larger than the males of a similar age. Sexual maturity is reached at the age of 18–20 months (i.e. October) when the average carapace length in the males is 16 mm. and in the females 17–18 mm. It seems possible, however, that the males reach maturity somewhat in advance of the females.

A few prawns live on to a fourth year, reaching a carapace length of 23–24 mm. but the numbers are very small and insufficient for inclusion.

SUMMARY

Pandalus bonnierii is a dioecious species and no protandrous hermaphrodites have been seen.

The breeding season and incubation period for *P. bonnierii* are described.

The number of eggs laid increases with the size of the female. At 16 mm. carapace length the number of eggs is *c.* 1000 and at 24 mm. carapace length the number of eggs is *c.* 4000. The number for a single mm. size group varies roughly by $\pm 10\%$.

Both male and female *P. bonnierii* become sexually mature at about 18 months, and in the Clyde seldom live beyond 3 years of age.

The colour of the eggs in *P. bonnierii* is sage green, in *P. borealis* blue green, in *P. montagui* light emerald green and in *P. propinquus* fawn.

Juvenile *P. bonnierii* can be separated into males and females by the shape of the pleopods within 4–6 months of hatching.

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