LIFE CYCLES AND SEASONAL MOVEMENTS OF
Cheirimedon femoratus (Pfeffer) AND *Tryphosella kergueleni* (Miers) (CRUSTACEA : AMPHIPODA)

By P. K. BREGAZZI*

ABSTRACT. Regular samples have been taken of two species of inshore sand-dwelling amphipod from the Antarctic.

Females of *Cheirimedon femoratus* mature 3 years after release and produce one brood of about 70 eggs with an incubation period of about 6 months. Males reach maturity 15–24 months after release. Males and females of *Tryphosella kergueleni* mature about 3 years after release and females may produce up to four successive broods, each of between 4 and 18 eggs, at intervals of about 6 months. Growth and development rates of both species are slow when compared with those of temperate amphipod species.

Over 90 per cent mortality occurs within the first year after release in *C. femoratus*, and rather less than this in *T. kergueleni*. There is negligible brood mortality in both species.

Both species are taken in flesh-baited traps in large numbers except for early-stage juveniles, ovigerous females of *T. kergueleni* bearing late-stage broods, and all ovigerous females of *C. femoratus*. A large proportion of plant material features in the diet of all stages of both species.

Although overlapping for much of their life cycles, ovigerous females of both species release their broods in areas separate from one another, thus avoiding competition for food during the early juvenile stages. All categories of *T. kergueleni* appear to undergo a movement away from the brood release areas during winter, perhaps in response to a diminished food supply. A movement during winter is less pronounced in *C. femoratus* and appears to be restricted to developing females.

The life cycle of *C. femoratus* is closely linked to the seasonal pattern of primary production, but that of *T. kergueleni* displays a large measure of independence from it.

GAMMARIDEAN amphipods are a conspicuous part of the inshore benthos of Antarctic regions. The great majority of investigations up to the present have been taxonomic, with nearly 250 species having been described from the Antarctic Peninsula, Weddell Sea and islands of the Scotia arc (Thurston, 1970, 1972) but information is now accumulating on the biology of Antarctic amphipods (Pearse, 1963; Thurston, 1968, 1970, 1972; Bone, 1972).

The family Lysianassidae contains many important Antarctic species and they have been collected extensively. This paper concerns aspects of the breeding biology of two species of inshore sand-dwelling lysianassids and forms part of a programme undertaken from December 1967 to April 1969 at Signy Island, South Orkney Islands.

The South Orkney Islands lie on the Scotia Ridge at the northern limit of the Weddell Sea. Signy Island (lat. 60°43′ S., long. 45°38′ W.) is a rocky island about 6·5 km. by 5 km., rising to 275·5 m., half of which is covered with a cap of permanent ice and snow. Coastal areas may be ice- and snow-free for several weeks in the summer. Sea-ice conditions are variable. Pack ice is common and fast ice may be present up to 7 months in a year, especially in sheltered coastal areas. Mean annual air temperature is about −4° C and mean monthly sea temperatures are given in Table I.

TABLE I. MEAN MONTHLY SEA TEMPERATURE (°C), BORGE BAY, SIGNY ISLAND, AT A DEPTH OF 8–10 m. (UNPUBLISHED DATA, M. G. WHITE AND D. G. BONE)

January	+0·20	July	−1·85
February	+0·38	August	−1·82
March	−0·22	September	−1·70
April	−0·43	October	−1·35
May	−1·22	November	−1·02
June	−1·86	December	−0·01

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In common with other Antarctic areas, the littoral zone at Signy Island suffers extensive ice scour during winter and is faunistically impoverished except for species which manage to survive in crevices. In summer, some algal growth occurs and mobile organisms, notably the limpet *Patinigera polaris* (Hombron and Jacquinot), are found (Walker, 1972). At this time, algae and sponges are apparent beneath stones and boulders, providing cover for some nemerteans, polychaetes, molluscs and crustaceans.

Below the littoral zone, the presence of large brown algae (*Desmarestia menziesii* J. Agardh, *D. anceps* Montagne and *Phyllogigas grandifolius* (A. et E. S. Gepp) Skottsberg) allows development of a richer fauna including nemerteans, polychaetes, molluscs, numerous amphipods, isopods of which *Glyptonotus antarcticus* Eights is conspicuous, the echinoderms *Sterechinus neumayeri* (Meissner) and *Odontaster validus* (Koehler) and fish (Price and Redfearn, 1968). The slower-growing sessile forms such as hydroids and brachiopods are restricted to crevices and overhangs on account of the continued but reduced scouring effect of ice floes.

At depths greater than about 25 m., where the effects of ice are further lessened, assemblages of bryozoans and sponges are dominant where substrate conditions allow.

The inshore bottom conditions include exposed bedrock, areas of boulders, moraine deposits, gravels, sand and mud. In deeper offshore waters, mud and silts predominate.

MATERIAL AND METHODS

The present investigation took place in Borge Bay on the east coast of Signy Island and mainly in or near Factory Cove, a small shallow inlet 200 m. long and 200 m. at the mouth (Fig. 1). The cove has a uniform bottom of fine sand sloping gently towards the mouth, and a depth varying from about 5 to 10 m. It is bordered by a narrow sloping rim of loose stones and boulders, with a sparse cover of brown and red algae, and harbouring a variety of polychaetes, molluscs, crustaceans, etc. The sandy bottom contains burrowing amphipods in large numbers, and also includes polychaetes (e.g. *Capitella* spp.), bivalves (e.g. *Yoldia* (*Aequiyoldia*) *eightsii* (Couthouy), *Mysella charcoti* (Lamy)) and isopods (e.g. *Serolis polita* Pfeffer). The amphipod species common in the sand are *Cheirimedon femoratus* (Pfeffer), *Tryphosella kergueleni* (Miers) (Fig. 2), *Pontogeneiella brevicornis* (Chevreux), *Parharpinia*
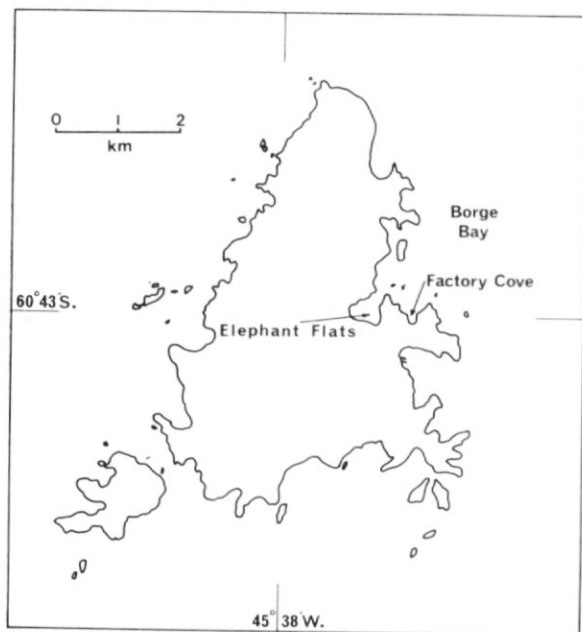

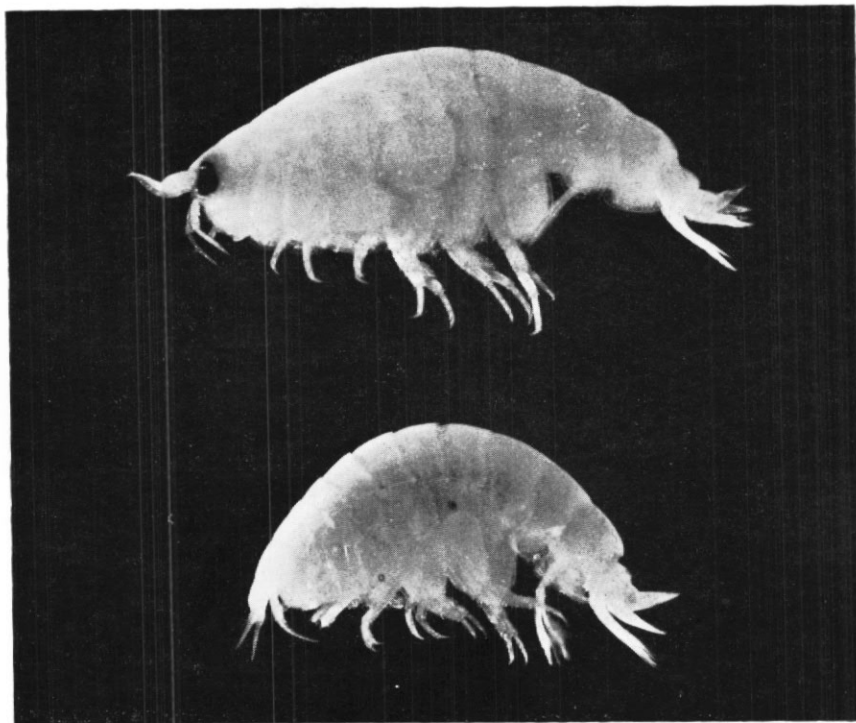Fig. 1. Outline map of Signy Island, South Orkney Islands.

Fig. 2. Ovigerous females of *Cheirimedon femoratus* (upper) and *Tryphosella kergueleni* (lower), ×5·25. (Red eye pigment lost from *T. kergueleni* during fixation.)

rotundifrons Barnard and, to a lesser extent, *Lepidepecreum cingulatum* Barnard and *Monoculodes scabriculosus* Barnard. None of these species makes permanent burrows and all are restricted to the top layer of light-coloured sand which lies 2–3 cm. deep over a darker mass of undetermined depth.

   C. femoratus was described by Pfeffer (1888) as *Anonyx femoratus* and a detailed description was also given by Chevreux (1905) as *C. dentimanus*. It has usually been recorded from sandy bottoms but occasionally also from stony or rocky areas. Its distribution extends from South Georgia, through the South Sandwich Islands and the South Orkney Islands to the South Shetland Islands and the Antarctic Peninsula, and also at Terre Adélie on the Antarctic mainland; its bathymetric range has been recorded from littoral to 310 m. (Thurston, 1972). In the present study, most specimens were taken from between 5 and 20 m., but a single male was included in a trawl over a silty bottom at 230 m. A few specimens were found amongst small stones in the boulder rim of Factory Cove.

   T. kergueleni was described by Miers (1875) as *Lysianassa kergueleni* and has since received at least five synonyms. It has been recorded from gravel, sand and mud, is circum-polar in distribution and has been taken from 5–750 m. (Thurston, 1972). In the present study, it was taken mainly in sand but also gravel to a lesser extent, and some specimens were found amongst littoral stones in Factory Cove.

   Material was obtained by aqualung divers from two sampling sites near the entrance to Factory Cove, one near the boulder edge and the other half-way across. Each site was about 20 m. by 20 m. Samples were collected in 10 cm. by 25 cm. cylindrical tins similar to those described by Everson and White (1969), open at one end and covered by fine nylon mesh at the other, which were pressed into the bottom sand by hand. The tins were gently dug out, reversed and placed in a suitable crate for carrying. Material from the tins was sieved in seawater through 0·5 mm. mesh, which retained all stages of amphipods. These were preserved in

5 per cent formalin in sea-water, neutralized with excess calcium carbonate. Ovigerous females were preserved separately in order to avoid egg loss during preservation and storage.

Material from the two sampling areas showed no obvious differences and so they have been considered together as "site A" (Fig. 3). 20–30 10 cm. cores were obtained during the first week of each calendar month from January 1968 to March 1969 inclusive.
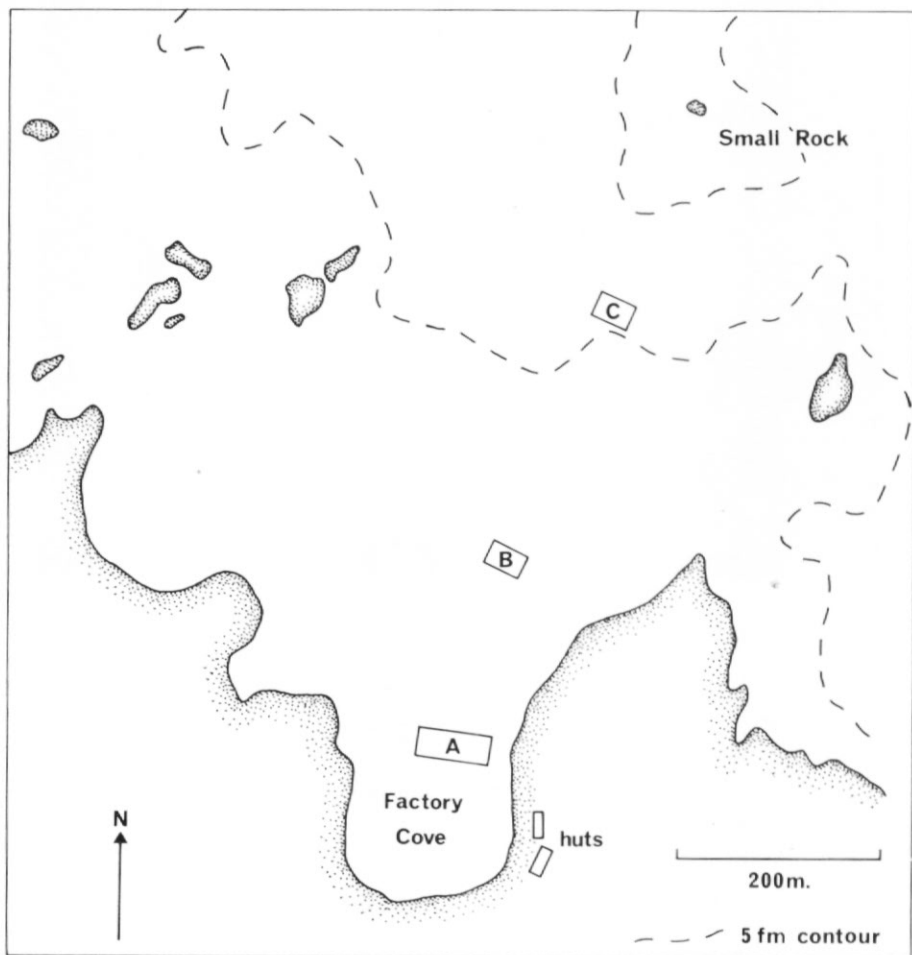

Fig. 3. Map of part of Borge Bay, Signy Island, showing sampling sites A, B and C.

Specimens of amphipods from each core were identified, sexed and measured to the nearest 0·5 mm., from the tip of the rostrum to the base of the telson along the dorsal mid-line. Animals without oostegites (female) or genital papillae (male) were regarded as juvenile. The smallest size category used was up to 2·5 mm. Eggs were removed from the brood pouches of ovigerous females, counted and assigned to one of five arbitrary developmental stages (Table II), based on those of Thurston (1968) for *Bovallia gigantea* Pfeffer. A few hatched juveniles

TABLE II. ARBITRARY DEVELOPMENT STAGES FOR AMPHIPOD BROODS

I: Yolk cells, but no non-pigmented embryonic tissue.
II: Embryonic tissue partly or wholly enveloping yolk cells.
III: Caudal furrow and limbs present.
IV: Eye rudiments present and appendages complete.
V: Brood hatched, at least in part.

from brood pouches were measured under a binocular microscope to the nearest 0·1 mm. Most animals were measured after several months in formalin.

Additional material was obtained from the main sampling area and from several other sites at various times by:

i. A small hand dredge, consisting of a steel frame 30 cm. by 15 cm., with nylon mesh bag attached, which was scooped through the surface sand by an aqualung diver. This same dredge was also used to gather animals swimming in open water by night.

ii. 13 cm. by 7 cm. polythene jars with short tubes attached into which, by squeezing and releasing, selected individual animals could be sucked up.

iii. Polythene funnel traps, with nylon mesh sides, baited with fish or penguin flesh. Two sizes of trap were used, large (30 cm. by 15 cm.) and small (15 cm. by 9 cm.).

iv. A 46 cm. diameter plankton net towed behind a small boat by night to obtain swimming specimens from 1 to 5 m. below the surface.

v. A 4 ft. [1·16 m.] Agassiz trawl, also towed behind a small boat.

The main sampling sites in Factory Cove were permanently marked on the sea bottom by large steel cans weighted with stones. Positions of all sampling sites were established by one or more of the following methods:

i. Prismatic compass bearings were taken from fixed points on land to either set buoys or holes cut in the sea ice and marked by ice blocks, depending upon conditions.

ii. Back bearings were taken from the sampling site to prominent fixed points on land.

iii. Prominent land marks were "lined up" from the sampling site.

iv. A portable echo depth-sounder was used in conjunction with the appropriate Admiralty chart.

Material for histological examination was fixed in neutral sea-water formalin or sea-water Bouin's fluid, embedded in paraffin wax (m. pt. 54·5° C), and sectioned at 8 μm. Sections were stained with Heidenhein's haematoxylin and counter-stained with eosin.

Cheirimedon femoratus (Pfeffer)

Breeding, growth and maturity

Ovigerous females are encountered throughout the year, but counts of numbers taken and examination of brood stages reveal a clear annual cycle (Fig. 4a and b). The small total number of stage I broods is accounted for by the relatively short duration of this developmental stage. Eggs are laid in the brood pouch during March–June. Development takes about 6 months and hatching (stage V) occurs during August–December, with a peak in October. It was not always possible to decide, by size alone, whether juveniles from the first size group (up to 2·5 mm.) in a sample were free-living or had been dislodged from the brood pouch during collection. Feeding whilst within the brood pouch must be very rare and largely fortuitous, because, of the several hundred juveniles examined from brood pouches, only 26 from two separate broods were noted with such gut contents. Therefore, the presence in the gut of food particles, other than yolky material, is a good indication of a free existence. By this criterion, most juveniles began their free existence in December and this was about 2 months after the peak of hatching within the brood pouch (Fig. 5). This suggests that hatched broods may be retained within the brood pouch until feeding conditions are favourable, whereupon they are released.

Some hatched young are likely to be lost from the brood pouch on account of their own activity, but it seems likely that most are released from a given brood at one time by specific behaviour of the female. This was observed a few times in glass dishes in the laboratory, and when a female was occasionally disturbed beneath the surface of sand, also in the laboratory. The body of the female is extended and the first antennae forced upwards and backwards. The first pair of gnathopods extend forwards, whilst peraeopods 5, 6 and 7 point posteriorly. The second gnathopods and peraeopods 3 and 4 remain passive. The second antennae twitch somewhat, held in a normal position and the pleopods extend posteriorly, quivering slightly.

During this process, the oostegites are held apart and the young, very active, are enabled to
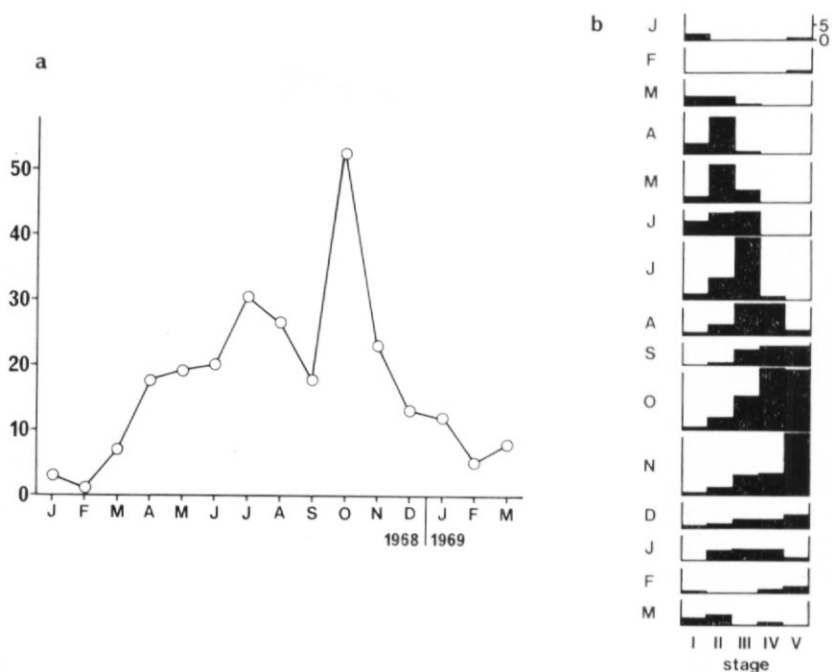
Fig. 4. a. Mean numbers of ovigerous *C. femoratus* in ten core samples for each monthly sample (site A).
    b. The same mean numbers of ovigerous *C. femoratus* expressed as brood development stages I–V
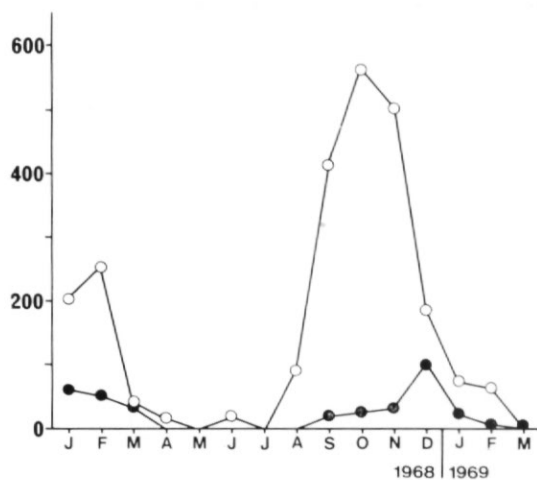   (Table II).

Fig. 5. Numbers of 2·5 mm. juveniles of *C. femoratus* per ten core samples in each monthly sample (site A).
    ○ Guts empty.   ● With gut contents.

escape from the brood pouch. The female soon recovers and appears to behave normally following release of the brood.

The small range of size of young in the brood pouch ($2\cdot1$–$2\cdot3$ mm. with mean of $2\cdot20$ mm. for 125 individuals from five broods) and the complete absence of any exuvia, shows that moulting and growth does not take place before release. Free-living young within the size range $2\cdot1$–$2\cdot3$ mm. are also found in the field. There is, however, a slight increase in size following hatching, as the integument, initially soft, becomes more robust within a day or so. 66 young which were just hatched from five separate broods, had a mean length of $2\cdot14$ mm.

Mean monthly length/frequency diagrams for the 15 monthly samples are given in Fig. 6. Compared with most temperate species of amphipod, growth is slow throughout development and during winter months it apparently ceases. 1 year after release, juveniles have grown about 2 mm. to $4\cdot5$ mm. Males can be recognized at the earliest at this length, but more usually from 5 mm., by rudimentary genital papillae on the posterior margin of the sternum of peraeon segment 7. 18 months after release, males are about 7 mm. and 12 months later they have grown $2\cdot5$ mm. to about $9\cdot5$ mm. Most males do not survive beyond 36 months after release but a few appear to do so, reaching a maximum size of 12 mm.

Maturity in males is indicated by the presence of sperm strands issuing from genital papillae in preserved specimens and by the appearance of calceoli on the flagella of the first and second antennae.

Sperm strands are not present in all mature preserved specimens but they appear with increasing frequency as the animals increase in size (Fig. 7a). They are found throughout the
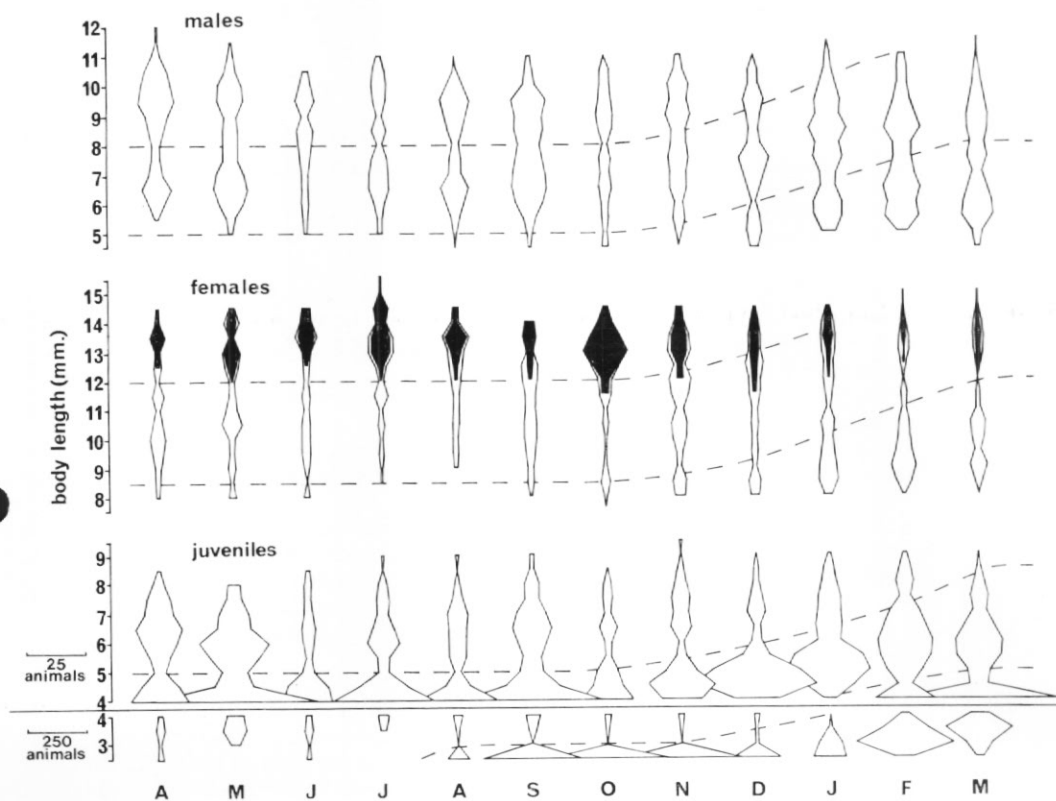

Fig. 6. Mean monthly length/frequency diagrams for numbers of *C. femoratus* per ten core samples, January 1968–March 1969 (site A).
Black areas, ovigerous females; broken lines, suggested boundaries between different age groups.
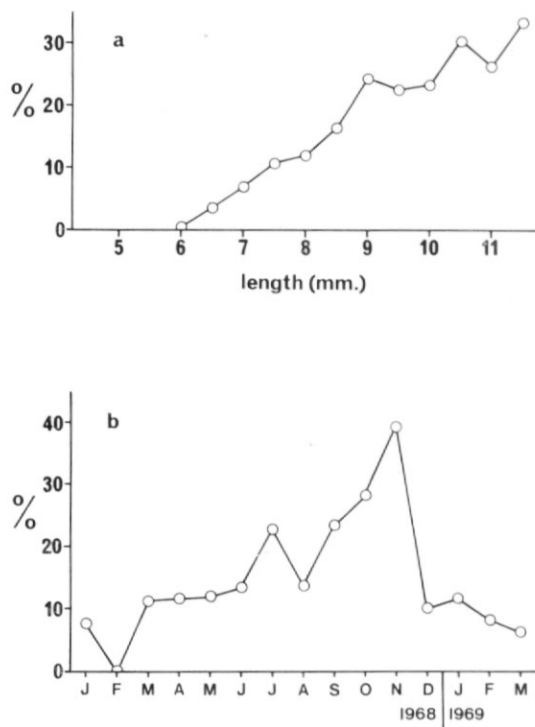
Fig. 7. a. Percentage of male *C. femoratus* of different sizes possessing sperm strands, from all monthly samples (site A).

b. Percentage of male *C. femoratus* (6·0 mm. and above) possessing sperm strands, for each monthly sample (site A).

year but in the present investigation greatest numbers occur in the November sample (Fig. 7b). Males achieve maturity well before maximum size is reached, between 15 and 24 months after release, depending upon the time of year, and during the spring this may occur at 6 mm., although animals are usually somewhat larger.

Histological sections confirm maturity at this stage by the presence of sperm in the testes and seminal vesicles.

At 6 mm., one to three calceoli may also first appear on each of the first and second antennal flagella, and these increase in number as additional flagellar segments are formed at successive moults (Fig. 8).

Similar structures have been shown in male *Gammarus duebeni* Lilljeborg to be associated with the sensing of water-borne odours from mature females of the same species (Dahl and others, 1970) and it is likely that they have the same role in *C. femoratus*, enabling the mature males to seek out mature females. Presence of large calceoli on the antennal flagella was also used by Hynes (1955) to determine maturity in *Crangonyx pseudogracilis* Bousfield (as *C. gracilis* Smith).

Four pairs of rudimentary oostegites appear simultaneously on the inner surface of the coxae of peraeon segments 2–5 in females at about 8 mm., 2 years after release. Growth proceeds for about another year, with the oostegites increasing in relative size with successive moults, before maturity, indicated by fully developed oostegites with setae, is reached at about 13 mm.

After mating and deposition of brood, no further growth occurs. Of the nearly 600 females with setose oostegites examined, only four were in the pre-brood state, indicating that the final moult to maturity precedes the act of brood deposition by a very short interval, as is the case with most aquatic amphipods.
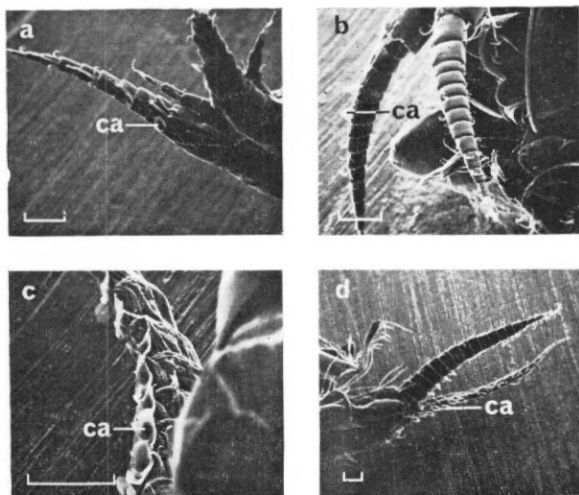
Fig. 8. a and b. Stereoscan micrographs of *C. femoratus*, male, length 6·5 mm.
   a. 1st antennae; b. 2nd antennae.
   c and d. *C. femoratus*, male, length 9·5 mm.
   c. 1st antenna; d. 2nd antennae.
   ca calceolus.
   Scale 0·1 mm.

16 post-ovigerous females were present in a sample taken by night from the sand surface and in open water during December. The margins of limbs, branchiae, oostegites and sternites of all except two were blackened and deformed to a greater or lesser extent. Degeneration of oostegites and branchiae in older individuals has been reported in *Bovallia gigantea* (Thurston, 1970) and in *Pontoporeia affinis* Lindström and *Pallasea quadrispinosa* G. O. Sars (Mathisen, 1953). Two of the post-ovigerous *C. femoratus* were in the process of being eaten, and all had empty fore-guts, except one which was taken in open water. The small number (20) of post-ovigerous females taken throughout the year in monthly samples suggests that, once a brood is released, the female does not survive for more than a short time.

Growth curves, summarizing most of the above information, are given in Fig. 9.

No suggestion can be offered as to why the greatest proportion of males with sperm strands occurs in November and yet females do not lay broods until March–June. The interval between copulation and deposition of brood is very short in most amphipods. Copulation occurs after the final moult of the female and eggs must be laid before the cuticle, and hence the genital aperture, hardens (Hynes, 1955). In semi-terrestrial amphipods the interval is somewhat longer, between 4 hr. and 4 days depending upon the species (Williamson, 1949).

Fecundity

A length/frequency graph for ovigerous females from all samples is shown in Fig. 10 and gives a mean length of 13·02 mm. The normal distribution suggests survival to produce only one brood, and further evidence for this is provided by the examination of a few hundred ovigerous females of different brood stages by dissection, sectioning and direct observation, all of which has failed to reveal any trace of developing oocytes or ova. As might be expected, therefore, there is no distinct "interbrood" condition such as has been described in *Gammarus pulex* (L.)* and *G. fasciatus* Say (Hynes, 1955) and *G. duebeni* (Kinne, 1952)*, in which the oostegite setae are lost, and in *Bovallia gigantea*, an Antarctic species in which the oostegite setae are partially lost (Bone, 1972).

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* In view of the current uncertainty of the status of the genus *Rivulogammarus* (see Stock, 1967), the more common usage of *Gammarus pulex* and *G. duebeni* has been retained throughout this paper.
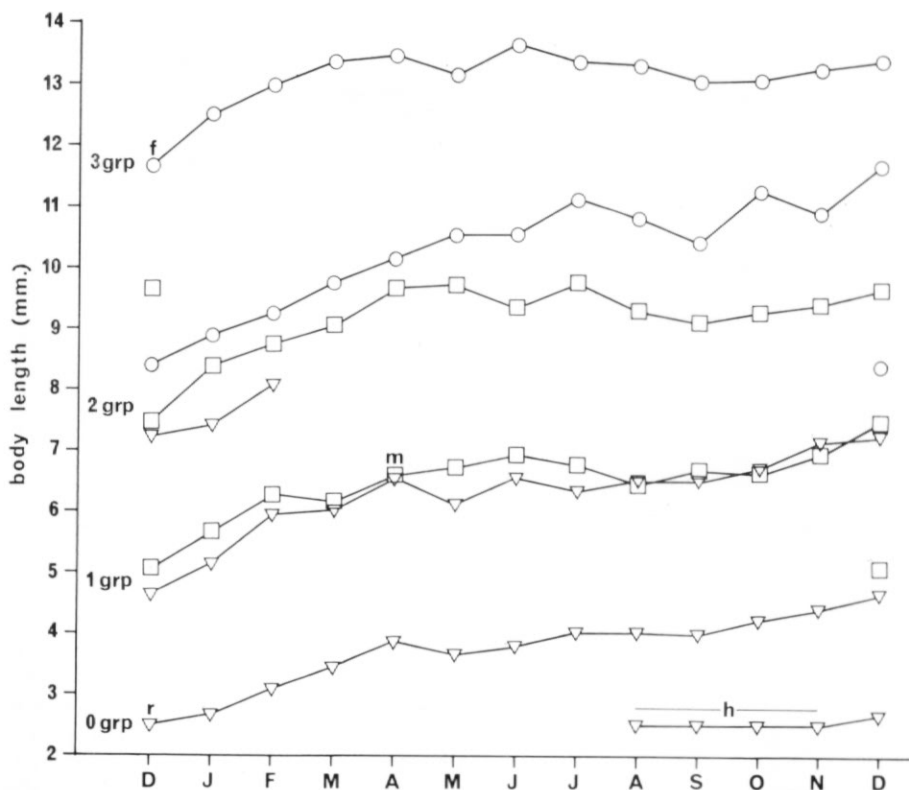
Fig. 9. Growth curves for *C. femoratus*, based on age groups for all monthly samples (site A), expressed as running averages for 3 monthly periods.
▽ Juveniles.   □ Males.   ○ Females.
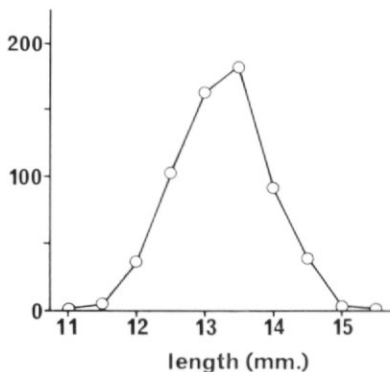h hatch; r release from brood pouch; m males mature (earliest); f females mature.

Fig. 10. Total numbers of ovigerous *C. femoratus* of different sizes from all monthly samples (site A). Total = 626 individuals.

There appears to be a negligible mortality of developing embryos within the brood pouch (Fig. 11). The apparent increase in numbers of eggs between stages I and II can be accounted for by the inadequate sampling of females with stage I eggs, this being due to the relatively short duration of this developmental stage.
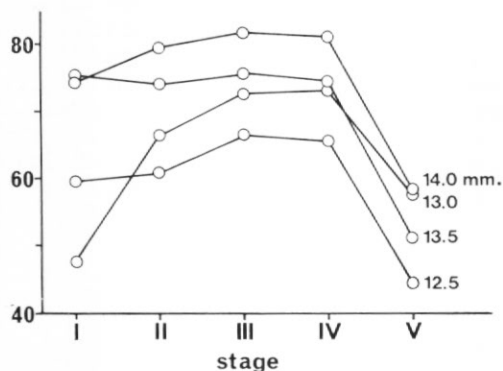

Fig. 11. Mean numbers of eggs/embryos of different developmental stages (Table II) in brood pouches of ovigerous *C. femoratus* of 12·5, 13·0, 13·5 and 14·0 mm. length, from all sources. Total number of females = 463.

The sharp decline in numbers at stage V (embryos hatched) is likely to be due in part to some hatchlings being lost by their own activity, but also to the handling of the female during collection. The brood is more readily jettisoned by the female at stage V than at earlier stages. A similar drop in brood numbers after hatching has been reported by Hynes (1955) for *Gammarus pulex* and *G. lacustris* Sars.

The mean numbers of egg/embryos of stages I–IV for each size of female are given in Fig. 12. This shows that there is a linear relationship between size of female and egg number, as has been reported for several malacostracan species (Jensen, 1958; Vlasblom, 1969; Thurston,
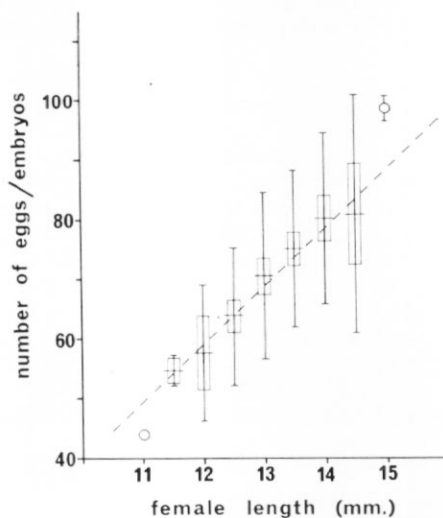

Fig. 12. Mean numbers, of eggs/embryos (stages I–IV) of ovigerous *C. femoratus* of different lengths (site A). One standard deviation (line) and two standard errors (rectangle) are shown on either side of the mean. (Regression line, $y = 9\cdot709x - 57\cdot315$, calculated for females 12·0–14·5 mm. in length.) Total number of females = 466.

1970). An ovigerous female of *C. femoratus* of mean length (about 13·0 mm.) will produce a mean brood of about 70 eggs.

Sex ratios

The total number from each age group of each mean monthly sample has been compared in order to establish sex ratios. Genital papillae appear in males at 4·5–5·0 mm., and it has been assumed that all males in the first size group here considered (6·5–7·0 mm.) are recognizable as such and that all "juveniles" are therefore females. At this stage, the male to female ratio is about 1 : 2 (Fig. 13). A greater number of females is not surprising since they grow larger, take longer to reach maturity and live longer than males. However, in succeeding months the relative number of females drops steadily, until at about the middle of "2 group" the ratio is reversed. Soon after the onset of "3 group" the males die and the females achieve maturity.
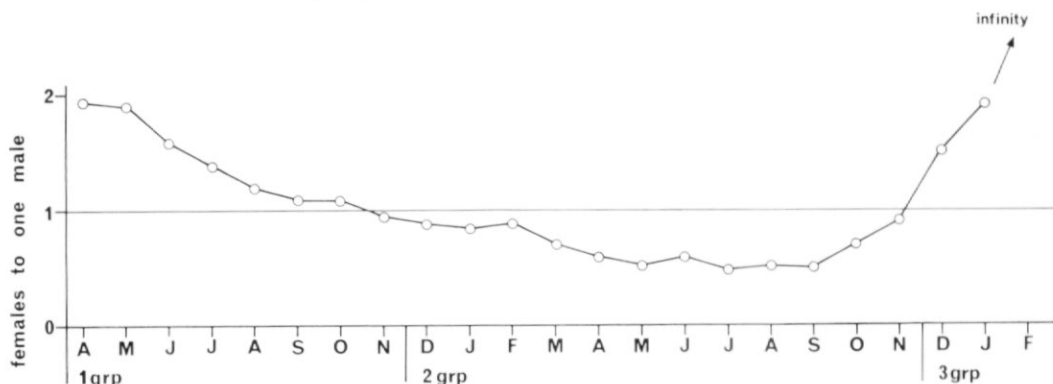

Fig. 13. Ratio of females of *C. femoratus* to one male for successive months and age groups (site A), expressed as running averages for 3 monthly periods.

In view of the longer life of the females, the steady decline in numbers relative to males is unexpected. Reference to Fig. 6 shows that this is probably a decline in absolute numbers also, for there are considerably fewer immature females taken than ovigerous females, particularly during the winter months.

The larger numbers of ovigerous females cannot be accounted for by their breeding for a second season, for it has already been shown that, in this species, females are most likely to produce only one brood in a lifetime.

The possibility is suggested, therefore, that at least some immature females move away from the sampling area, particularly during winter, returning to mate and release young.

Owing to the longer time of development to maturity in females, they will mate with males which are up to 18 months younger. In the first 3 months of the period when females achieve maturity, the ratio of mature males to mature females is 2·55 : 1. During March–June, when deposition of broods largely occurs, the ratio is 2 : 1. The preponderance of mature males ensures fertilization of all available females in spite of the absence of pre-copula. The survival of mature males over two breeding seasons indicates that they can mate more than once, but whether they can do so during one breeding season is not known. Male *Austrochiltonia subtenuis* Sayce are able to mate with more than one female. Having fertilized a female, they enter pre-copula with another almost immediately (Lim and Williams, 1971).

Mortality

In the present study, release of young from the brood pouch occurred mainly in December. Survival has been calculated by comparing mean total numbers in successive year groups for the mean monthly samples from November to January. The numbers for "0 group" include both recently released juveniles and embryos of stages III–V still within the brood pouches of ovigerous females. Embryos of stages I and II are considered to be part of the following year's

release. It has been assumed that the mortality rates of recently released female and male juveniles are the same, and that the 2 : 1 sex ratio apparent about the middle of "1 group" (Fig. 13) also applies at the time of release.

A very high mortality rate is indicated for the first year of growth (Fig. 14), with a much lower one in successive years. Females appear to have a slightly higher mortality than males, but this effect may really be due to the partial migration of females suggested above.

Known predators of *C. femoratus* are the fish *Notothenia* (Barnard, 1932), *Glyptonotus antarcticus* (personal communication from M. G. White), and the cape pigeon, *Daption capensis* L. (Beck, 1969). It is also likely to feature in the diet of other fish, various worms and amphipods, and perhaps young seals (Laws, 1956).
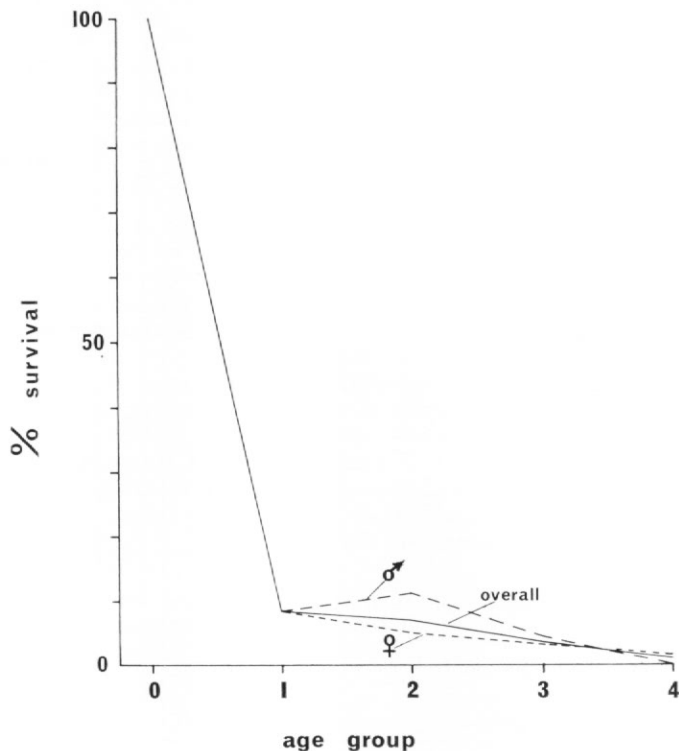

Fig. 14. Percentage survival of successive age groups of *C. femoratus* (site A). Pecked line, female; dashed line, male; solid line overall.

Diet

The stomach contents of over 100 animals have been examined, both fresh and preserved, representing all times of the year, all size groups and both sexes.

Stomachs of juveniles of about 5 mm. and below usually contain an unidentifiable greenish mass, doubtless algal in origin, in which diatom frustules are often present.

Thereafter, polychaete chaetae (*Capitella* spp.) and parts of small crustaceans occasionally appear, and the animals are readily taken in flesh-baited traps. It is possible, of course, that these amphipods are not actually predaceous and that the animal remains are ingested along with sand particles and diatoms.

Sand particles, diatoms and other algal remains are present in the stomachs of representatives of all classes throughout the year, but especially in summer, when the pronounced phytoplankton bloom occurs.

Adult specimens taken at 1–5 m. below the surface at night-time during the summer had full

stomachs containing a variety of planktonic algae, together with copepods and euphausiid larvae which also occur in the plankton at this time. Many ovigerous females were also included in these mid-water samples and all of them (30) had stage V (hatched) broods. In view of the fact that over 90 per cent of females with hatched broods taken in sand samples had empty stomachs, it seems likely that some stage V females exhibit a burst of swimming and feeding activity immediately prior to release of the brood. Empty stomachs were also frequently found in near-mature non-ovigerous females, in which the ovaries were approaching maximum size and virtually filling the thoracic cavity.

Adult specimens of both sexes, introduced into a sand/diatom mixture in the laboratory and subsequently examined, showed a high proportion of diatoms and relatively few sand grains in the stomach. Evidently, the animals can sift sand particles for food, the rows of setae on the first and second maxillae doubtless assisting this process.

Enormous numbers of animals can be taken throughout the year in traps baited with fish, seal or penguin flesh. Many more are caught by this means during the night when the animals are active, than during the day when they lie buried in the top 2 cm. or so of sand.

A liquid of homogenized fish, squeezed from a polythene bottle over the bottom surface during the day, brings many amphipods of different species from the sand. Individuals of *C. femoratus* swim towards the odour source, except for ovigerous females which, upon emerging from the sand, swim rapidly away from the odour before re-burrowing.

Ovigerous females are rarely taken in baited traps, and those taken all bear early stage eggs.

The forsaking of a flesh diet by ovigerous females can be considered a measure which protects the developing brood, since cannibalism regularly occurs and particularly when a mass of amphipods is swarming around a piece of carrion. Amphipods of the same and other species, when damaged during collection, are readily attacked and eaten by *C. femoratus*. Cannibalism was often noted in laboratory tanks.

Ovigerous females are seen out of the sand on the bottom surface by night, and feeding largely continues until the embryos approach mid-point of development. The amount of food material in the stomach of the females is easily seen by viewing from the ventral side after the brood has been removed (Table III). Examination of the stomach contents of ovigerous females reveals plant cellular material, diatoms, sand grains and the usual unidentifiable greenish mass, almost certainly algal remains. The mouth parts of ovigerous females are identical with those of large non-ovigerous females.

TABLE III. PERCENTAGES OF OVIGEROUS *C. femoratus* WITH EMPTY, PART FULL AND FULL FORE-GUTS, BEARING BROODS AT DIFFERENT STAGES

Brood stage	Fore-gut empty	Fore-gut part full	Fore-gut full	Number of animals
I	48·94	36·17	14·89	47
II	33·33	37·12	29·55	132
III	60·92	28·16	10·92	174
IV	85·82	12·69	1·49	134
V	91·24	6·57	2·19	137
				624

(Combined data from 15 monthly samples.)

Young *C. femoratus* below 4 mm. are rarely taken in traps and it is likely that they avoid carrion for the same reasons as do the ovigerous females. As already noted, feeding by young while in the brood pouch is of negligible occurrence. Cannibalism by pre-release juveniles was noted on three occasions, eating out their dead parent, and each other.

To summarize, *C. femoratus* is a versatile omnivore/predator, probably having a preference for carrion when available, except in the early juvenile and ovigerous stages when an algal diet occurs. Feeding virtually ceases during the late ovigerous stages.

Tryphosella kergueleni (Miers)

Breeding, growth and maturity

Males and females of *T. kergueleni* are identifiable by the appearance of genital papillae and oostegite rudiments respectively, at 6·5–7·0 mm. Length/frequency diagrams based on the 15 monthly samples obtained from the main sampling area in Factory Cove (site A) are shown in Fig. 15.
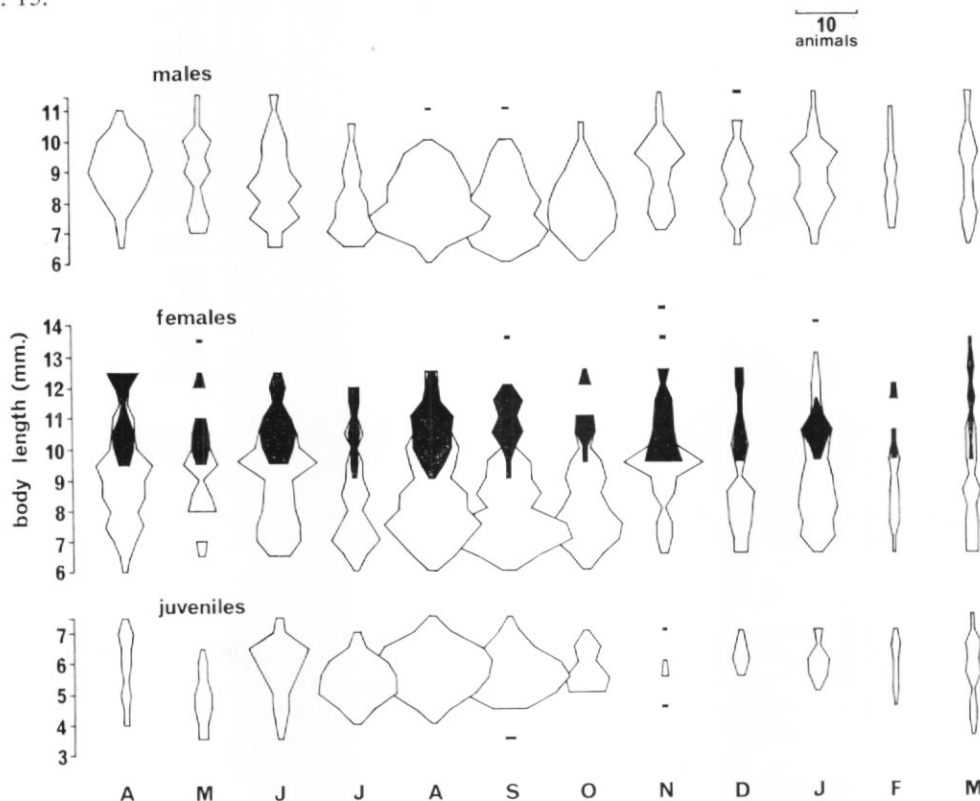

Fig. 15. Mean monthly length/frequency diagrams for numbers of *T. kergueleni* per ten core samples, January 1968–March 1969 (site A).
Black areas, ovigerous females.

It is apparent that easy identification of age groups and periods of maximum growth, such as is possible in the case of *C. femoratus*, cannot be done for *T. kergueleni*. The main features of interest are that many more specimens of all categories were taken in winter than in summer, with a peak during August, and that there is a complete absence of recently hatched and released animals, which in this species have been assigned to a size category of up to 3·0 mm. in length. Ovigerous females are found throughout the year, also with a maximum in the August sample, but every such female taken carried eggs of stages I, II, III and never later stages, no matter what time of year they were collected (Fig. 16a and b).

Between 20 October and 6 December 1968, 16 hand dredge samples were obtained from different parts of Borge Bay in an attempt to locate ovigerous females of *T. kergueleni* carrying stage IV and V broods. Some females with such late-stage broods were present in all these samples, except in those taken from within, or at the entrance to Factory Cove, where, as expected, only females with early stage broods were found (Fig. 17).

These facts are most readily interpreted as indicating a seasonal movement of males, females
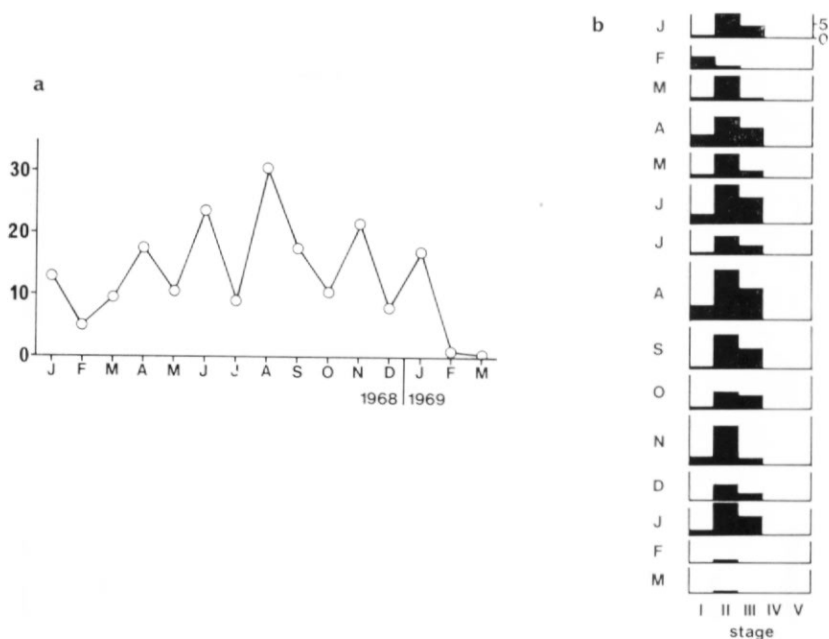
Fig. 16. a. Mean numbers of ovigerous *T. kergueleni* in ten core samples for each monthly sample (site A).
       b. The same mean numbers of ovigerous *T. kergueleni* expressed as brood development stages I–V
          (Table II).

and juveniles of this species into the main sampling area (site A; Fig. 3) and Factory Cove during winter, and a movement out of the area during early summer. Ovigerous females may move away from the sampling area at any time of the year, but before a late stage of embryo development in the brood pouch is reached, so that young are hatched and released elsewhere.

Total numbers of ovigerous females taken in the monthly samples from site A show a peak at 10·5 mm. (Fig. 18). The skewed appearance of the graph no doubt indicates survival of ovigerous females to produce more than one brood, with an increase in size between broods.

So that the breeding cycle of this species could be more fully studied, hand-dredge bottom samples were obtained well outside Factory Cove in a sandy area known to include late-stage ovigerous females (site B; Fig. 3). Samples were taken from May 1969 to February 1970, and amphipods were retained by sieving and treated as before. A 25 cm.³ portion of all amphipod material was taken from each monthly sample and specimens of *T. kergueleni* were measured and sexed.

The numbers of the smallest category of free-living juveniles (3 mm.), expressed as a percentage of total numbers of juveniles per month, are shown in Fig. 19a. Thurston (1972) has suggested that females of this species, once mature, may breed continuously and may produce two broods per year. This is borne out by the present study, with one brood group being released in winter and one in summer. The frequency distribution of ovigerous females taken, expressed as a percentage of total numbers of females for each month, also has bimodal properties (Fig. 19b).

The numbers of females with different stages of brood development each month (Fig. 20) confirm that breeding is not confined to one brood release per year. The twice annual breeding pattern suggested above is not obvious. However, the greatest numbers of females without broods but having fully developed oostegites do occur at about the times of the two periods of brood release. No ovigerous females or early stage juveniles of *C. femoratus* were found in the samples from site B.
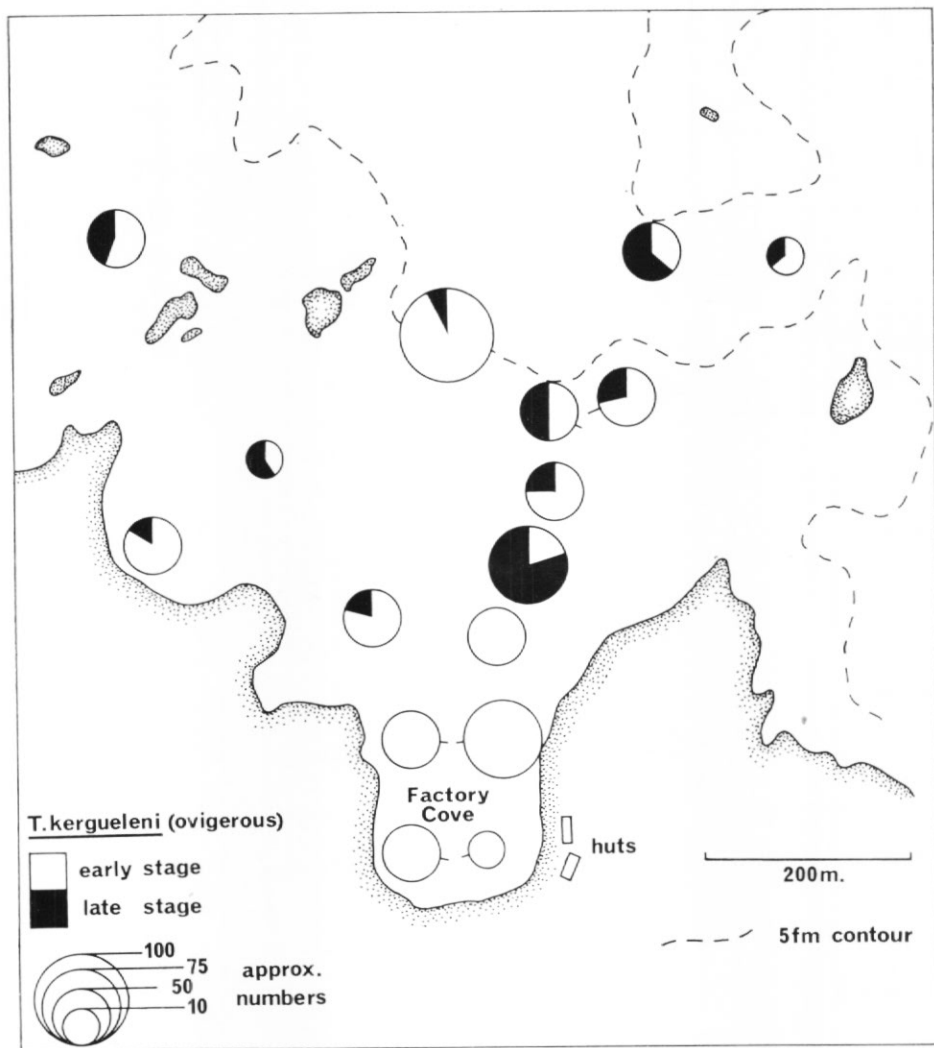
Fig. 17. Numbers of ovigerous *T. kergueleni* of early (I–III) and late (IV–V) stages, taken from different sites in Borge Bay between 20 October 1968 and 6 December 1968.
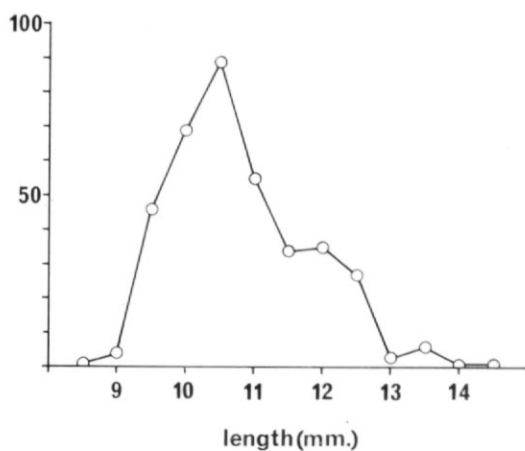
Fig. 18. Total numbers of ovigerous *T. kergueleni* of different sizes from all monthly samples (site A). Total = 371 individuals.
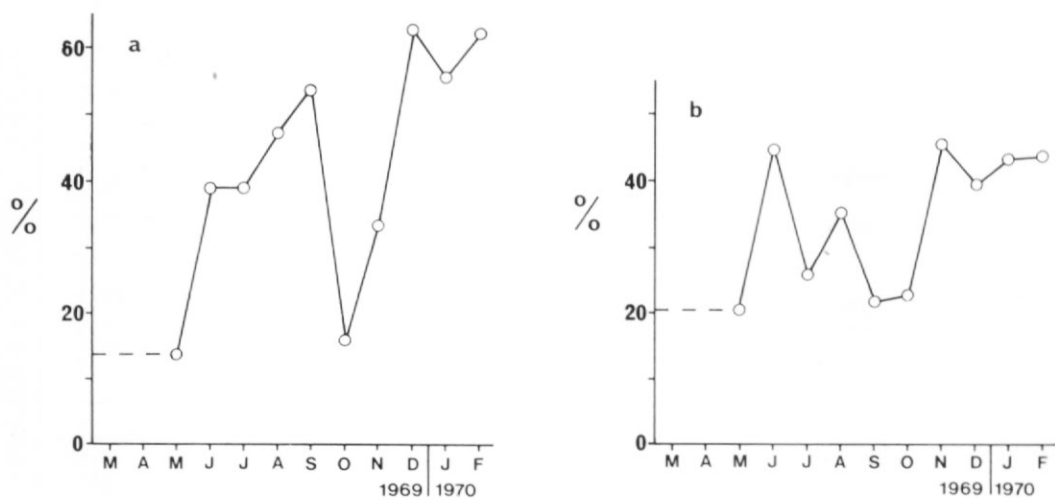
Fig. 19. a. 3 mm. juveniles of *T. kergueleni*, expressed as percentage of all juveniles, from each monthly sample (site B).
b. Ovigerous females of *T. kergueleni*, expressed as percentage of all females, from each monthly sample (site B).

Fig. 20. Numbers of ovigerous *T. kergueleni* from site B with different brood development stages (Table II). i with fully developed oostegites but no brood; ns no sample.

The main monthly samples (site A; Factory Cove) of ovigerous females of *T. kergueleni* do not show bimodal characteristics (Fig. 16a) such as has been indicated for those from site B, whether considered in absolute numbers or as a percentage of total adults. The suggested seasonal winter migration, however, would obscure th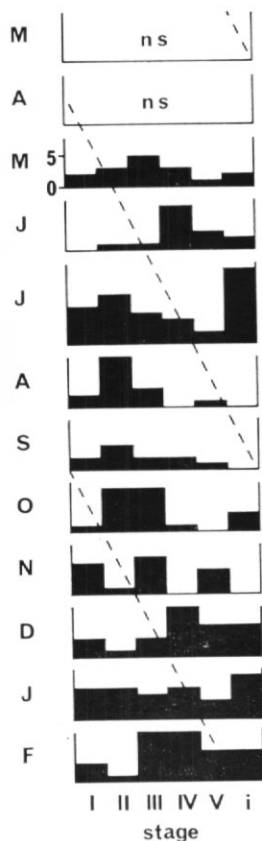e twice annual breeding pattern. This migration, perhaps a response to diminished food supply in winter, accounts for the greatest number of ovigerous females being taken at site A during August, animals which would produce the summer brood release. The winter brood release is produced by females which will carry stage I, II and III eggs during the summer when there is abundant food and so no great pressure to move out from the breeding area, thereby accounting for the unimodal pattern of total ovigerous females obtained from within Factory Cove (Fig. 16a).

A development time in the brood pouch from laying to hatching of about 6 months, as is the case with *C. femoratus*, would allow the production of two broods per year. The small proportion of females without a brood (15·2 per cent of all those bearing setose oostegites) suggests a development time which is only a little less than 6 months given two broods per year, and laboratory studies on egg development (Bregazzi, 1973) suggest that both of these species develop at similar rates.

Length/frequency data for all specimens of *T. kergueleni* taken at site B are shown in Fig. 21. Again, there are no obvious size groups or growth trends, but these are likely to be obscured by there being two brood-release periods each year, and also, the samples are not strictly quantitative, being taken with a hand dredge.
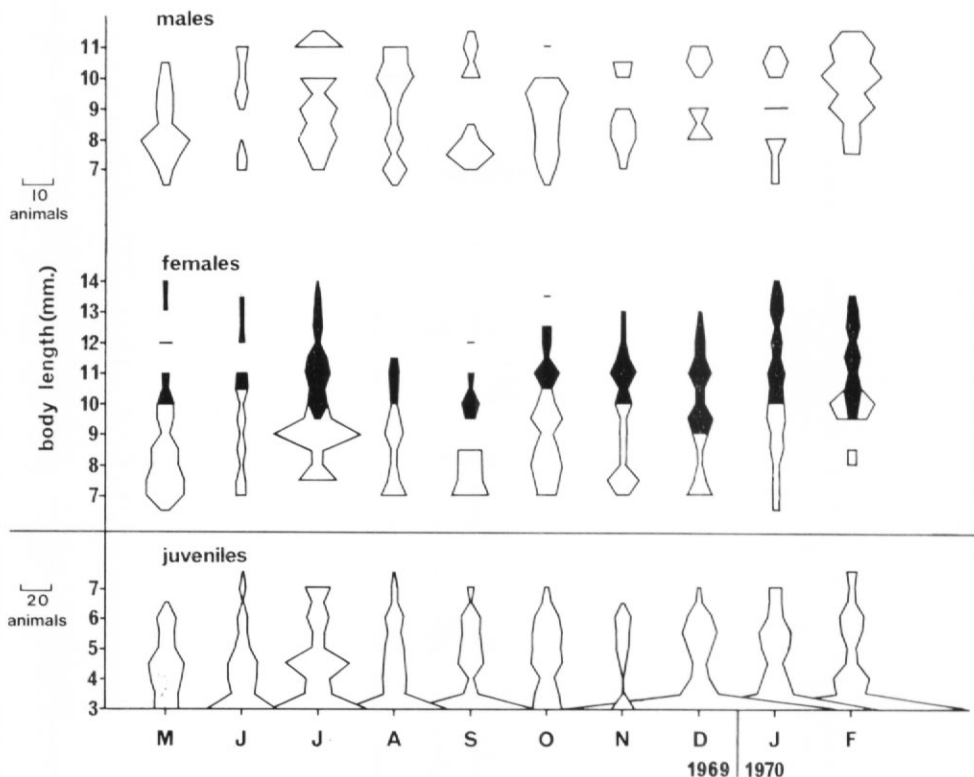
Fig. 21. Length/frequency diagrams for *T. kergueleni* for each monthly sample (site B).

As with *C. femoratus*, there is no evidence to suggest growth or moulting within the brood pouch. 60 juveniles from six different brood pouches had a mean length of 2·64 mm. and individuals of this size also occur free-living in the field. Feeding does not take place within the brood pouch.

In order to estimate growth rates, total numbers of all categories have been taken for each period corresponding to a brood release (i.e. June–September and November–February). These data, together with suggested year groups, are shown in Fig. 22.

It appears that males may live up to about 4 years and females somewhat longer. Determination of maturity in males is based on the presence of calceoli which are borne on the flagella of both antennae, as in *C. femoratus*, and appear at 9–9·5 mm., that is about 3 years after release (Fig. 23). Unlike *C. femoratus*, the second antennal flagella grow in size and segment number more rapidly than the first, and they are more than twice as long as the first when the animal reaches full size (11·5 mm.). Histological sections confirm the presence of mature sperm in testes and seminal vesicles at 9 mm., but not earlier. As with *C. femoratus*, therefore, maturity is reached before maximum size is obtained, but in *C. femoratus*, as has been shown, it occurs relatively much earlier. Sperm strands were found in only ten male *T. kergueleni*, at 10–11·5 mm.

Females of *T. kergueleni* reach maturity from about 9–9·5 mm. onwards, as indicated by large oostegites with setae and, usually, a brood. Maturity appears to occur about 3 years after release, as is the case with males. The higher percentage of mature females without broods at site B (15·2 per cent) than at site A (1·73 per cent) suggests that mating usually takes place in the areas where broods are released.
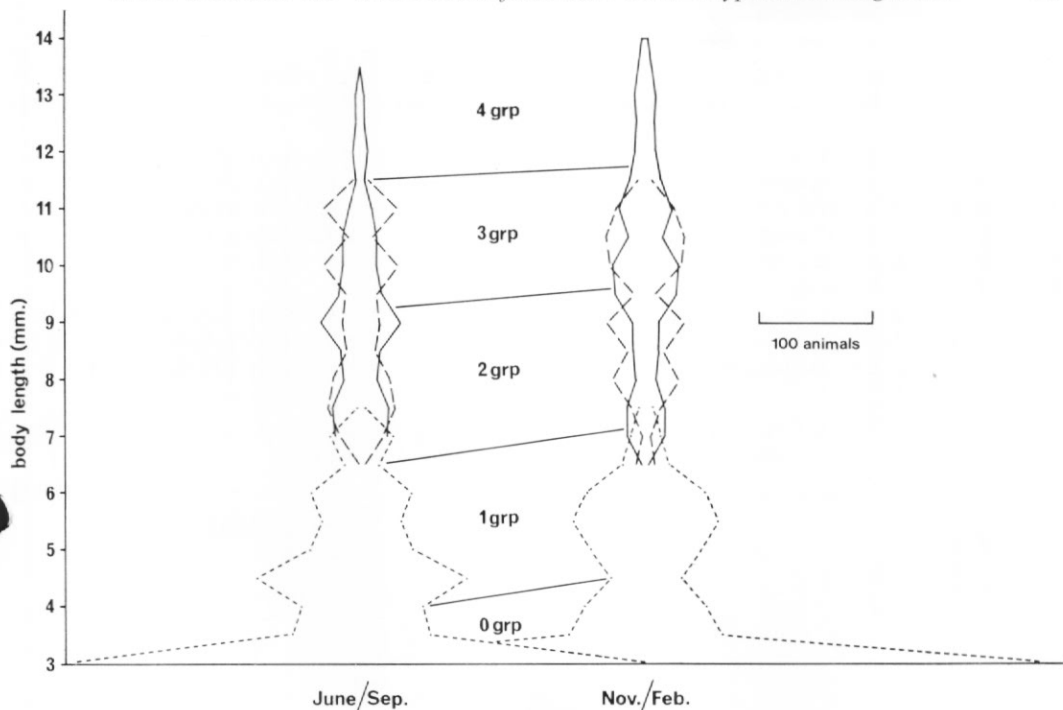
Fig. 22. Total numbers of *T. kergueleni* of different lengths for periods corresponding to each brood release, with estimated year groups (site B).
Dotted line, juveniles; dashed line, males; continuous line, females.
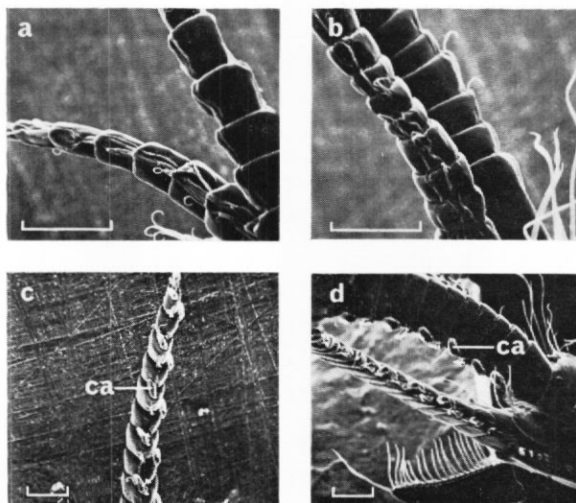
Fig. 23. a and b. Stereoscan micrographs of *T. kergueleni*, male, length 8·5 mm.
a. 1st antennae, with setae but no calceoli;
b. 2nd antennae, with setae but no calceoli.
c and d. *T. kergueleni*, male, length 12·0 mm.
c. 1st antenna; d. 2nd antennae.
ca calceolus.
Scale 0·1 mm.

Fecundity

The mean number of eggs/embryos of stages I–IV for each size of female are given in Fig. 24. As with many crustaceans, there is a linear relationship between size of female and number of eggs.

It has already been indicated that, owing to the skewed nature of the length/frequency graph for ovigerous *T. kergueleni* (Fig. 18), they may survive to produce more than one brood. Examination of several individuals shows that this is the case, for the ovaries of females with broods are found to contain developing ova. The ova are especially clear in fresh specimens with late-stage broods, arranged in two longitudinal rows, pale to dark orange in colour, beneath the dorsal integument.

By direct counting of the ova, the probable size of the next brood can be determined, dissection only being necessary in the case of preserved specimens. By reference to Fig. 24, the length of the female at the next brood can be estimated. From these data (Table IV), it is seen

TABLE IV. MEAN NUMBER OF DEVELOPING EGGS IN BOTH OVARIES OF
OVIGEROUS FEMALES OF *T. kergueleni* BEARING BROODS
AT DEVELOPMENT STAGES IV AND V

| Length (mm.)	Number of animals examined	Mean number of developing eggs in ovaries	Range	Estimated length of female at next brood (nearest mm.)
9·5	3	9·67	8–12	12·0
10·0	8	9·25	8–10	12·0
10·5	12	11·67	8–14	13·0
11·0	4	12·25	10–14	13·0
11·5	7	13·29	11–16	13·5
12·0	9	14·22	11–16	14·0
12·5	4	16·50	14–18	?
13·0	3+1*	14·00	12–16	14·0
13·5	4+3*	15·75	14–17	?
14·0	2	21·50	20–23	?

* Number of animals with wholly or partially degenerate ovaries, not included in means or ranges.

that a female may survive to produce three successive broods, with an increase in size between each brood. Many of the largest females contain developing ova in the ovaries in numbers that suggest no further increase in size of the female at the brood or broods which follow the third. Also, as some of these animals contain a proportion of atrophied or undeveloped ova, it is probable that, even if a female survives to produce a fourth brood, it will be the final one.

No females longer than 11·0 mm. were found with oostegites partially setose or without setae, and it is concluded that no distinct "interbrood" condition occurs in females of *T. kergueleni*. Those of 11 mm. and below bearing oostegites without setae would, of course, give rise in due course to the first generation of ovigerous females.

The small numbers of large females without broods (38 compared with a total of 556 ovigerous females) show that the summer and winter brood releases are not the result of breeding by alternate groups of females.

As with *C. femoratus*, there is negligible mortality of developing embryos within the brood pouch (Fig. 25), and the drop in numbers at stage V can likewise be attributed to activity of the hatched juveniles and also handling of the female during collection, although, being a smaller brood, the latter does not happen to the same extent as in *C. femoratus*.

Sex ratios

In both males and females, genital papillae and oostegite rudiments respectively appear at about 6·5–7·0 mm., and maturity is attained at about 9–9·5 mm. The sex ratios of identifiable males to females of 8·5 mm. or smaller are about equal at site A and also at site B. For mature
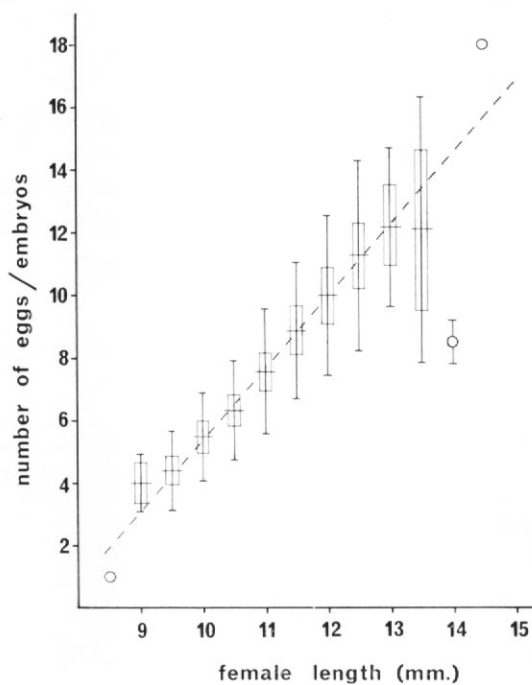
Fig. 24. Mean numbers, of eggs/embryos (stages I–IV) of ovigerous *T. kergueleni* of different lengths (all sources). One standard deviation (line) and two standard errors (rectangle) are shown on either side of the mean. (Regression line, $y = 2 \cdot 275x - 17 \cdot 343$, calculated for females $9 \cdot 5$–13 mm. in length.) Total number of females = 786.
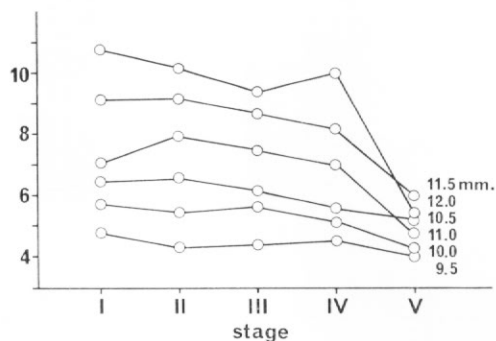
Fig. 25. Mean numbers of eggs/embryos of different development stages (Table II) in brood pouches of ovigerous *T. kergueleni* of $9 \cdot 5$, $10 \cdot 0$, $10 \cdot 5$, $11 \cdot 0$, $11 \cdot 5$ and $12 \cdot 0$ mm. in length, from all sources. Total number of females = 813.

animals (9 mm. and larger), however, there is a preponderance of females at both sites A and B, and this can be accounted for by the longer life span of the females (Fig. 26a and b).

At site A, the greatest proportions of mature females occur during the period of the suggested winter movement into this area (Fig. 26a). This points to the greater need for females to accumulate food reserves for reproductive purposes than males, as has been suggested for *C. femoratus* which also shows signs of a winter movement of females.

Supporting the possibility of a movement of greater numbers of females than males in *T. kergueleni* is the fact that the lowest proportions of females at site B are found during the period of highest proportions at site A (Fig. 26b).

That mature males may have less tendency to undergo a seasonal movement than females also supports the suggestion already made that mating takes place usually in the same areas in which broods are released in this species.

It follows from the longer life of females, in which more than one brood is produced, that males are capable of mating with more than one female.

Mortality

Accurate quantitative samples representative of the entire life cycle of *T. kergueleni* are not available. Survival has been estimated from total numbers of individuals in successive year groups using data from Fig. 22. Numbers for "0 group" include in this case, developing embryos from the brood pouches of ovigerous females of stages III–V which are assumed to belong to the same generation as the smallest free-living juveniles. A 1 : 1 sex ratio has been assumed at the time of release.
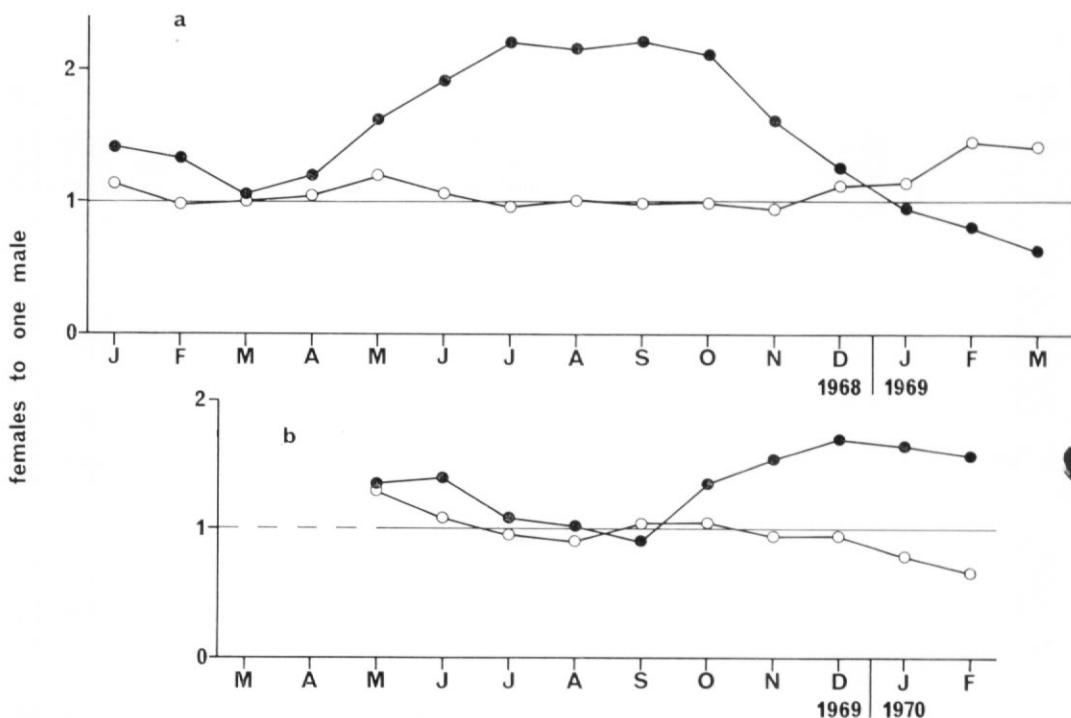

Fig. 26. Ratio of females of *T. kergueleni* to one male for successive months.
  a. From site A.
  b. From site B.
  (Running averages for 3 monthly periods.)
   ○ Lengths 8·5 mm. and below. ● Lengths 9·0 mm. and above.

The percentage survival of successive year groups compared with "0 group" are shown in Fig. 27. There seems to be a high mortality rate during the first year after release (but not so high as that for *C. femoratus*) and a much lower one during the second and third years. Males are not represented in "4 group" and the number of females drops sharply during this time.

Known and likely predators of *T. kergueleni* are the same as those for *C. femoratus*.
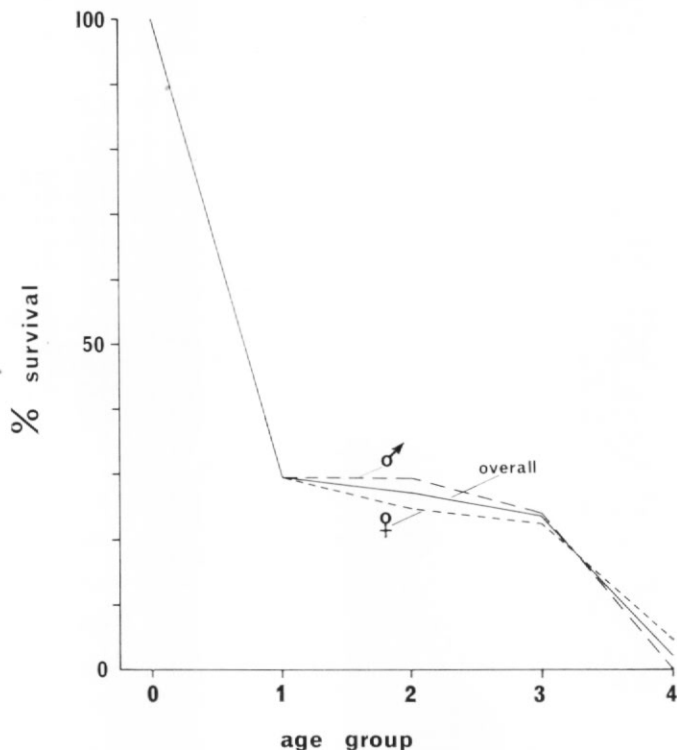
Fig. 27. Percentage survival of successive age groups of *T. kergueleni* (site B). Pecked line, female; dashed line, male; solid line, overall.

Diet

Fore-gut contents of over 100 specimens of all categories were found to be remarkably uniform over the year. Most contained an unidentifiable mass, brownish green in colour, and about three-quarters of these also included at least a few, but more often many, sand grains. Diatoms were very common, but algal chains and other plant cellular material appeared in only about 10 per cent of all specimens.

Small crustacean remains were present in the guts of only two specimens, as were a few polychaete chaetae.

About 20 per cent of all specimens had empty fore-guts and these occurred in summer as well as winter samples.

Large numbers, of stages other than very small juveniles, are caught in flesh-baited traps at all times of the year, especially at night. Ovigerous females are included in the traps up to about the mid stage of brood development, after which carrion is abandoned and feeding of any sort is very much reduced. The presence of numerous ovigerous females in traps, unlike *C. femoratus*, can be attributed to the necessity for accumulating food reserves in the developing ovaries in preparation for the succeeding brood.

T. kergueleni, whilst clearly able to take advantage of available carrion, appears to be primarily a bottom-deposit feeder, relying mainly upon diatoms and other small algae, and possibly detritus.

DISCUSSION

The rates of development and growth to maturity in *C. femoratus* and *T. kergueleni* are very slow, as is the case with other high-latitude species of amphipod, when compared with temperate species (Tables V and VI). The same is also true for many invertebrate poikilotherms (Ruud, 1932; Thorson, 1936; Dunbar, 1940, 1941, 1962, 1968; White, 1970).

TABLE V. DURATION OF BROOD INCUBATION IN POLAR
AND TEMPERATE AMPHIPODS

Antarctic		
Orchomene plebs	5 months	Pearse, 1963 (as *Orchomenella proxima*)
Bovallia gigantea	7 months	Thurston, 1970
	6–8 months, −2 to 1° C	Bone, 1972
Cheirimedon femoratus	6 months, −2 to 1° C	This paper
Tryphosella kergueleni	6 months, −2 to 1° C	This paper
Arctic or boreal		
Parathemisto libellula	several months	Dunbar, 1957
Gammarus wilkitzkii	5–6 months	Barnard, 1959
Pontoporeia affinis	3–4 months, 3–4° C	Mathisen, 1953
Pallasea quadrispinosa	2–2½ months	Mathisen, 1953
Temperate		
Gammarus pulex	3 months (winter)	Hynes, 1955
	16–17 days (summer)	Sexton, 1924
Gammarus duebeni	19–20 days 20° C	Forsman, 1951
	47–49 days 4–6° C	
	12·5 days 20° C	Kinne, 1953
	19 days 14° C	
	14 days 18° C	Hynes, 1954
	54–59 days 4·7° C	
Gammarus lacustris	2 months (first brood, field)	Hynes, 1955
	20–22 days 18° C	
Gammarus fasciatus	16 days 16° C	Hynes, 1955
	7 days 24° C	
	9 days 20° C	Clemens, 1950
	22 days 15° C	
	41–45 days 10° C	
Gammarus locusta	9–10 days (summer)	Sexton, 1924
Gammarus zaddachi	10 days 20° C	⎰ Kinne, 1960 (as *G. salinus*)
	15 days 14° C	⎱ Kinne, 1961 (as *G. zaddachi*)
Marinogammarus obtusatus	13 days 6–9° C	Sheader and Chia, 1970
Crangonyx pseudogracilis	48 days 3·5° C	Hynes, 1955 (as *C. gracilis*)
	14–17 days 15° C	
	8 days 23° C	Embody, 1912
Corophium volutator	about 17 days (laboratory)	Watkin, 1941

The effect of temperature on growth and development rates in Crustacea is well documented, with higher temperatures inducing faster growth, within limits (e.g. Sexton, 1924, 1928; Kinne, 1953, 1960, 1961; Hynes, 1954, 1955; Patel and Crisp, 1960; Eltringham, 1967; Holdich, 1968). Dunbar (1968) cited examples of poikilotherms which are known to have slower growth to maturity in higher latitudes (viz. *Sagitta elegans* Verrill, *Thysanoessa raschi* M. Sars, *Pandalus borealis* Kroyer, *Calanus finmarchicus* Gunnerus, the Arctic char *Salvelinus alpinus* (L.), the Atlantic cod *Gadus morhua* L.).

It was once widely held that the slow growth rates of polar poikilotherms was a direct result of the low environmental temperatures. However, it is now known that the metabolic rates of many Arctic marine poikilotherms are not nearly so different from those of equivalent forms in temperate and tropical regions as might be expected from environmental temperature considerations (Thorson, 1936, 1952; Dehnel, 1955; Kinne, 1963). Also, it can be readily observed that polar marine species are just as active in their movements as their counterparts from lower

TABLE VI. DURATION OF GROWTH FROM HATCHING (OR RELEASE) TO
MATURITY (ABLE TO BREED) IN POLAR AND TEMPERATE AMPHIPODS

Antarctic		
Orchomene plebs	18 months	Pearse, 1963 (as *Orchomenella proxima*)
Bovallia gigantea	28–29 months (m)	Thurston, 1970
	41–42 months (f)	
	14–17 months (m)	Bone, 1972
	40–42 months (f)	
Cheirimedon femoratus	15–24 months (m)	This paper
	36 months (f)	
Tryphosella kergueleni	36 months (m, f)	This paper
Arctic or boreal		
Pontoporeia affinis	2 years	Mathisen, 1953
Pallasea quadrispinosa	8 months	Mathisen, 1953
Temperate		
Gammarus pulex	4 months	Hynes, 1955
	70 days (summer)	Sexton, 1924 (calculated by Hynes, 1955)
	180 days (winter)	
Gammarus locusta	35 days (m)	Sexton, 1924
	38 days (f)	
Gammarus lacustris	7–10 months	Hynes, 1955
Gammarus fasciatus	3 months (summer)	Hynes, 1955
	6 months (winter)	
	13 weeks (16° C)	
	6 weeks (23° C)	
Gammarus chevreuxi	36–40 days (summer)	Sexton, 1928
	2–4 months (winter)	
Gammarus zaddachi	30+ days (m) 19–20° C	{ Kinne, 1960 (as *G. salinus*),
	20–30 days (f)	1961 (as *G. zaddachi*)
Corophium volutator	4 months, or less (summer)	Watkin, 1941

m Male; f Female.

latitudes. Dunbar (1968) suggested that high activity at low temperature may be achieved only at the expense of other processes requiring energy, such as growth.

Thorson (1936), Fox and Wingfield (1937), Scholander and others (1953) and Démeusey (1957) have shown that the oxygen consumption of several cold-water poikilotherms is much higher than that of similar, and in some cases the same, species from warmer waters at a given temperature, and Dehnel (1955) found that the larvae of three species of gastropod from Alaska developed from 2 to 9 times faster than larvae of the same species from California, at a given temperature. (See also review by Bullock (1955).)

It is very likely, therefore, that the slow development and growth of many polar marine species are not directly due to the low environmental temperatures, with which the metabolism of these species can apparently cope. The high selective value of genetic adaptation of the metabolism of polar marine poikilotherms suggests that it is most likely to be of general occurrence, and the most important determining factor for growth rates is thought to be the seasonal nature of primary production which is consequent upon the conspicuously oscillating environment. In this context, it is of interest that the few species of pelagic larvae in Arctic waters possess remarkably rapid growth rates (Thorson, 1950).

Dunbar (1968) has advanced the suggestion that the evolution of polar marine ecosystems has been and is influenced by two major selective and antagonistic processes. One promotes ecosystem stability by the proliferation of species, the lowering of specific fecundity (thus reducing the amplitude of population oscillations) and the spreading of food consumption and breeding over as much of the year as possible. The other selects for adaptations to the seasonal oscillations, resulting in annual breeding cycles, slow growth, large populations with high specific fecundity, and a smaller number of species.

Dunbar considered that adaptation to the oscillating polar environment is well advanced in marine poikilotherms, and that adaptation to ecosystem complexity (and hence stability) is less so, but it is proceeding.

The majority of those species of polar benthic invertebrates that have been studied in detail possess breeding cycles that are clearly seasonal (Thorson, 1936, 1950; Pearse, 1963, 1966; Thurston, 1968, 1970, 1972; Bone, 1972), and some species with non-seasonal breeding habits are also known (White, 1970; Thurston, 1972).

In the light of these remarks, it is interesting to note that the life cycles of *C. femoratus* and *T. kergueleni*, both members of the same family and largely occupying the same type of habitat, differ in many important respects.

The life cycle of *C. femoratus* is clearly adapted to the seasonal environment, and the spring phytoplankton bloom in particular, by the young being liberated in the spring and summer. There is also evidence that the hatched broods are retained in the brood pouch for about 2 months or more, enabling them to be released at the time of maximum phytoplankton productivity, by a positive behavioural action on the part of the female. Larvae of *Balanus balanoides* (L.) are retained in the parental mantle cavity, and the time of their release is also thought to be determined in part by a response of the parent to the spring phytoplankton bloom (Moyse and Knight-Jones, 1967).

The ovigerous females of *C. femoratus* bearing hatched broods, which were swimming and feeding amongst the plankton during summer nights, may represent a means of dispersal of young.

The apparent cessation of growth in winter is most likely due to the seasonal reduction in food supply rather than the slightly lower temperatures at this time (Table I), as Bone (1972) has also pointed out for *Bovallia gigantea*. In view of the slow growth of these species, it is of interest that McLaren (1966) has calculated that the 2 year life cycle of *Sagitta elegans* in the Arctic gives definite advantages in fecundity and maintenance of numbers than if breeding took place at 1 year and at consequently smaller body size, assuming similar mortality rates.

The longer period of development to maturity in the females compared with males of *C. femoratus* may be accounted for by the necessity to lay down materials in storage organs and the developing ovaries, a process which extends over three summer seasons. The males, being smaller and with less reproductive material to accumulate, can thereby mature earlier, at 15–24 months, as appears to be necessary. The maturation of gonads is induced in female *Pontoporeia affinis* by the decreasing illumination in late summer (Segerstråle, 1970) and it is possible that this is also the means whereby synchrony of the breeding cycle is attained in *C. femoratus*. Mature male *C. femoratus*, however, are found throughout the year (Fig. 7b), and Bone (1972) likewise reported the presence of mature sperm in the seminal vesicles of *B. gigantea* at all times of the year.

Members of the family Lysianassidae are noted for their necrophagous habit (Hodgson *in* Walker, 1907; Enequist, 1949; Arnaud, 1970; Thurston, 1972) and so could be expected at least partly to be independent of a seasonal food supply. However, plant material features conspicuously in the diet of *C. femoratus* and is indeed obligatory for newly hatched young and most ovigerous females. In spite of the vast numbers of this species taken in flesh-baited traps, it seems that necrophagy is not so advanced (or perhaps the supply of corpses is not so abundant) as to allow freedom from the seasonal production of plant material. By the criteria of Dunbar (1968), the large number in a single brood of *C. femoratus* also reflects adaptation to the seasonal environment. Production of a large brood is aided by the reduction of storage organs and the lack of developing ova in the thoracic cavity of ovigerous females, allowing for a larger brood-pouch volume. Furthermore, the ventral integument of the female in the brood-pouch region is expanded and exceedingly thin, especially between segments and along the mid-ventral line. This is clearly an adaptation for a large brood, as is the case with *Glyptonotus antarcticus* (White, 1970). Rigid sternites, convex from the ventral aspect, are present in immature females up to the final moult before brood deposition.

In contrast to all this, *T. kergueleni* is not directly dependent upon the seasonal nature of the environment, although its breeding is apparently synchronized. First and foremost, two relatively small broods are produced per year, one in summer and one in winter. If this species is independent of the seasonal phytoplankton bloom, it follows that there is less advantage in

retaining hatched young for extended periods in the brood pouch. Of all the ovigerous females examined from areas where release was known to take place, only $9 \cdot 8$ per cent carried hatched broods compared with $20 \cdot 7$ per cent in the case of *C. femoratus* where, as has been suggested, there is an advantage in retaining a brood until maximum phytoplankton production is reached.

The gut contents of all categories of *T. kergueleni* are very uniform over the year, and the large variety and numbers of planktonic algae present in the spring and summer waters does not appear to be reflected in the diet at this time, which is contrary to the situation found in *C. femoratus*. This is also indicated by night samples from open water during the summer which frequently contained large numbers of actively feeding *C. femoratus*, but only very few *T. kergueleni*. Visual observations by night also support these remarks.

Large numbers of *T. kergueleni* can be taken in flesh-baited traps throughout the year, but it is not known how important necrophagy is for this species. Recently released juveniles and late-stage ovigerous females are never taken in traps. Enequist (1949), in a study of northern amphipod species, has suggested that a transition to a detritus diet from a meat or carrion diet seems likely in the Lysianassidae. The necrophagous habit may well have been unduly emphasized in the past for members of this family on account of the dramatic numbers obtainable in flesh-baited traps, particularly in the Antarctic.

The size of egg in *T. kergueleni* is larger than that of *C. femoratus* by a factor of $1 \cdot 38$ (Bregazzi, 1973) and, consequently, the juvenile is also larger. Assuming that the body proportions of the juvenile and mature female are the same, the increase in size from $2 \cdot 64$ mm. (hatched) to $10 \cdot 5$ mm. (first brood) represents an increase in body volume of about 60 times. For *C. femoratus*, the corresponding measurements are $2 \cdot 20$ and $13 \cdot 02$ mm., giving an increase in body volume of about 200 times. This means that the increase in body volume from hatching to maturity in *C. femoratus* females is about $3 \cdot 5$ times that in *T. kergueleni*. The females of both species mature about 3 years after hatching and therefore, of the two species, *T. kergueleni* has considerably smaller energy requirements for completing the process of growth to maturity. So the fewer and larger eggs, and smaller size at maturity, could be further important factors in allowing *T. kergueleni* relative freedom from the seasonal nature of environmental productivity. Thorson (1950) also stated that the greater the size of an individual at hatching, the smaller are its relative food and oxygen requirements.

If *T. kergueleni* was dependent on the seasonal environment to the same extent as *C. femoratus*, a similar conspicuous period of growth should be apparent during the spring and summer. Reference to Fig. 21 shows that this is not the case, although samples from site B may not be adequate, and indeed there are signs that growth proceeds relatively slowly throughout the year at least in juveniles (Figs. 15, 21 and 22). Larger samples would possibly clarify the situation. A comparison of metabolic rates of *C. femoratus* and *T. kergueleni* in summer and winter would be of great interest.

It is possible to account for the earlier maturity of males in *C. femoratus* by the necessity to breed over two seasons on account of the greater numbers of females in this species. In *T. kergueleni*, however, the sex ratio approaches equality, and the males, although maturing at the same rate as the females, are sufficient in number to fertilize all mature females, and are likely to be able to do so twice a year, at an interval of about 6 months. This is again indicative of the spreading of reproductive effort over the year and the consequent relative independence from the seasonal environmental cycle.

T. kergueleni appears to have a lower mortality rate than *C. femoratus*, particularly during the first year of growth. If this is the case, it may be due to differences in habit or habitat as yet unknown but, also, a contributory factor may be the extension of breeding activity to two broods a year. The release of juveniles in *C. femoratus* occurs once a year during the summer when general productivity and hence predation is high. It is possible that, by releasing larger juveniles, in winter as well as summer, *T. kergueleni* undergoes less predation and is enabled to produce smaller broods. It is of interest that an expanded ventral integument in the brood-pouch region, such as is found in ovigerous *C. femoratus*, does not occur in ovigerous *T. kergueleni*.

Although the areas occupied by *C. femoratus* and *T. kergueleni* overlap for much of their life cycles, it is clear that juveniles are released in quite separate areas (see also Bregazzi, 1972).

Competition between these two species during the early stages of their life cycles, when food requirements are likely to be similar or even identical, is thus avoided.

That broods are produced in winter and summer in *T. kergueleni*, and that males and females probably mature at the same rate, may suggest the possibility of alternate generations being produced by two overlapping but not interbreeding populations in this species. Thurston (1972) recorded that *Pontogeneia antarctica* Chevreux has two incubations a year and females which have liberated young in October are apparently not able to breed again immediately. However, in *T. kergueleni* it appears that individual females can produce three or more consecutive broods, each at intervals of about 6 months, and so the possibility of alternate generations as described above is ruled out. Consequently, in the locality of the present study, *T. kergueleni* cannot be held to be undergoing speciation, in spite of the fact that some of the conditions for establishing alternate generations appear to have been fulfilled. In *C. femoratus* there is no such possibility either, as females must also regularly be fertilized by males of a different generation.

Changes in distribution associated with seasons have been recorded for many species of benthic and littoral Crustacea, for example *Carcinus maenas* L. (Naylor, 1962), the isopods *Eurydice pulchra* Leach and *E. affinis* Hansen (Jones, 1970) and three species of *Limnoria* (Eltringham and Hockley, 1961), the amphipods *Bathyporeia pilosa* Lindström and *B. pelagica* (Bate) (Fish and Preece, 1970), the European crab *Cancer* (Meek, 1916) and perhaps the Antarctic amphipod *Orchomene plebs* (Hurley) (Hodgson *in* Walker, 1907, as *Orchomenopsis rossi* Walker). The different patterns of seasonal movement in *C. femoratus* and *T. kergueleni* can best be viewed in relation to the suggested relative independence of *T. kergueleni* from the seasonal phytoplankton production.

There is less evidence for a seasonal movement in *C. femoratus* and it appears to be restricted to developing females. It is probably best considered as a foraging dispersal from the breeding area associated with the accumulation of food reserves and developing oocytes prior to attainment of maturity. It may have a seasonal component, for the smallest number of such females was found at the breeding area studied (site A) during the mid-winter preceding maturity, but it is possible that this lower density is due, at least in part, to the influx of large numbers of *T. kergueleni*.

A seasonal movement of all categories of *T. kergueleni* other than the smallest juveniles seems well established (Figs. 15, 16b and 26) and involves movement from the breeding area (represented by site B) during winter with a return in the spring. Some evidence suggests that particle size and hardness of substrate is important in determining distribution of this species (Bregazzi, 1972). The present study has not established whether an orientated migration takes place, or indeed whether the animals necessarily return to the same locality as they started from, and it may be a general non-orientated dispersal in more than one direction. In either event, a major dispersal during the winter when food is likely to be less plentiful is of obvious advantage to a species which breeds during the winter as well as the summer, and it must be of considerable importance in determining the nature of the breeding cycle in *T. kergueleni*.

The two species discussed in this paper, both members of the same family, can be considered to represent the two major adaptive trends in the polar benthic faunas as advanced by Dunbar (1968). Thus *C. femoratus* has growth, feeding, size of brood and time of release of young clearly synchronized with the annual cycle of primary production. *T. kergueleni*, with feeding, reproductive activities and perhaps growth spread over the year, indicates, together with smaller size of brood, relative freedom from seasonal oscillations, and so may be considered a positive contributor to the stability of the inshore benthic ecosystem.

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APPENDIX

Monthly trap samples

Information obtained from trap samples is limited because the contents of the sample are not likely to represent accurately the adjacent amphipod fauna. Young and ovigerous stages of some species may be absent from traps on account of their not being attracted to carrion. The area of influence of the traps used is not known and will depend upon water movements, the nature of the bait and the length of time the traps are in position. Furthermore, unless visible from the surface or inspected by divers, estimating the precise nature of the immediate surroundings of a trap in position is always attended by a certain amount of guess work. When drawing conclusions from trapping data, these limitations are borne in mind.

Methods

Large fish-baited traps were used to obtain samples at roughly monthly intervals from February 1968 to April 1969 near site A in Factory Cove and from April 1968 to April 1969 at a position mid-way between site B and Small Rock (Fig. 3). The depth of water at the latter position (site C) was about 10 m. and the bottom was composed of irregular patches of sand, algae and pebbles.

Traps were set before dark and left in position overnight for about 12 hr. The contents were almost entirely amphipods, usually many thousands in number, and a representative sample of these was preserved in 5 per cent neutral formalin. Each sample was thoroughly mixed and the amphipods in a 25 cm.^{3} portion, loosely shaken down, were identified and counted.

Results

The results, with each species expressed as a percentage of the total number of amphipods in a sample, are given in Table VII. The numbers for *C. femoratus* and *T. kergueleni* reflect the breeding habits of these species, as described above.

i. *C. femoratus*. There is a higher proportion of *C. femoratus* at site A, known to be a breeding area, than site C, and the few ovigerous females (ten) of this species all occur at site A. All have early stage eggs in their brood pouches. A few juveniles of 3·5–4 mm. were taken at both sites. Most of these occurred at site A during March–April, and the number over the entire sampling period was 9·51 per cent of the total for this species, compared with 1·20 per cent for similar animals at site C.

ii. *T. kergueleni*. The greatest proportion of *T. kergueleni* at site A was taken during August 1968, which is in agreement with the results of the core samples reported above. The percentage of ovigerous females of this species at both sites are about the same, being 38 per cent at site A and 38·9 per cent at site C. This is expected, on account of the movement described in this paper which is undertaken by both ovigerous and non-ovigerous adults.

iii. *Orchomene nodimanus* (Walker). This species occurs irregularly at both sites but a higher proportion was taken at site C. Other trap samples from deeper water between 30 and 40 m. contained much higher proportions of *O. nodimanus*, and over 90 per cent of the total number of amphipods in one case. The complete absence of this species from the bottom core samples at site A shows that it is not likely to be a burrower. The bottom conditions at site C are deeper and probably more favourable for this species.

iv. *O. rotundifrons* (Barnard). Four specimens occur in the samples from site A and 14 from site C.

v. *O. plebs* (Hurley). In spite of the small numbers of this species in the samples (36 from site A and 21 from site C), its virtual absence during the summer strongly suggests that

this is another species which undertakes seasonal movements, moving into shallow water during winter and returning to deeper water during summer. It is possible that the seasonal nature of the trapping data is the result of a change in feeding habits. This is considered to be unlikely, however, because large numbers of this species were taken during December 1968, feeding on a corpse of the fish *Chaenocephalus aceratus* (Lönnberg) (caught by E. Twelves) at about 200 m., showing that the necrophagous habit is retained during the summer.

Hodgson (*in* Walker, 1907) recorded large numbers of *Orchomenopsis rossi* Walker (now known to be chiefly *Orchomene plebs*, see Hurley 1965a, b) from traps at McMurdo Sound, and noted their complete absence during 25 October–27 December 1902. Also, he concluded that "these amphipods travel about the sea bottom in vast hordes in search of food". This species is common in traps in the Ross Sea (Littlepage and Pearse, 1962; Bullivant and Dearborn, 1967), and it has been taken at Terre Adélie (Arnaud, 1970).

TABLE VII. PER CENT DIFFERENT SPECIES OF AMPHIPOD IN A 25 cm.^{3} PORTION OF EACH MONTHLY TRAP SAMPLE

	C. femoratus (ovigerous)	*C. femoratus* (non-ovigerous)	*T. kergueleni* (ovigerous)	*T. kergueleni* (non-ovigerous)	*Orchomene nodimanus*	*O. plebs*	*O. rotundifrons*	*Lepidepecreum cingulatum*	*Pontogeneia antarctica*	TOTAL NUMBERS
Site A										
4 Feb. 1968	—	82·8	2·6	10·5	3·1	—	0·2	0·5	—	418
15 Mar.	0·2	92·1	1·9	5·6	0·2	—	—	—	—	518
Apr.	No sample									
7 May	1·6	89·6	1·1	4·1	2·3	1·3	—	—	—	387
16 Jun.	0·3	94·8	0·8	—	1·9	1·9	0·3	—	—	367
10 Jul.	0·5	92·7	—	0·8	2·5	2·9	0·3	0·3	—	373
1 Aug.	—	57·5	10·6	31·0	—	0·6	0·3	—	—	310
29 Aug.	—	96·8	1·9	0·9	—	0·2	—	—	0·2	432
23 Oct.	—	98·9	—	1·1	—	—	—	—	—	269
19 Nov.	—	63·0	10·7	21·0	5·3	0·3	—	—	—	310
16 Dec.	—	99·7	0·3	—	—	—	—	—	—	319
12 Jan. 1969	—	85·5	2·4	11·5	0·3	—	0·3	—	—	354
4 Feb.	—	99·7	0·3	—	—	—	—	—	—	336
4 Mar.	—	76·6	8·0	13·6	1·4	—	0·2	—	0·2	638
2 Apr.	—	94·3	0·5	0·5	2·2	2·5	—	—	—	363
MEAN PER CENT	0·20	87·42	2·94	7·74	1·48	0·75	0·12	0·06	0·03	
Site C										
12 Apr. 1968	—	70·8	1·2	9·1	18·1	0·8	—	—	—	265
12 May	—	21·8	10·7	48·0	15·3	1·9	2·3	—	—	262
2 Jun.	—	36·6	23·5	39·3	—	0·3	0·3	—	—	298
10 Jul.	—	85·0	—	8·2	3·4	3·0	0·4	—	—	233
Aug.	No sample									
8 Sep.	—	63·0	5·1	20·7	8·8	1·0	1·4	—	—	295
Oct.	No sample									
9 Nov.	—	79·9	4·6	14·3	0·8	—	0·4	—	—	261
3 Dec.	—	63·5	13·1	23·4	—	—	—	—	—	274
27 Dec.	—	76·5	7·0	16·5	—	—	—	—	—	273
4 Feb. 1969	—	49·5	11·6	18·0	20·9	—	—	—	—	206
Mar.	No sample									
2 Apr.	—	87·4	0·3	0·7	10·3	1·0	0·3	—	—	292
MEAN PER CENT	—	63·40	7·71	19·82	7·76	0·80	0·51	—	—	