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THE BIOLOGY OF SIX SPECIES OF ANOMURA (CRUSTACEA, DECAPODA) FROM RAUNEFJORDEN, WESTERN NORWAY

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ABSTRACT

Populations of six sympatric species, *Galathea intermedia, Pisidia longicornis, Pagurus bernhardus, P. cuanensis, P. prideauxi,* and *Anapagurus chiroacanthus* from two shallow sounds, were investigated during 18 months. Four types of bottom were distinguished. *G. intermedia* and *P. longicornis* were positively correlated with the amount of coarse substrate mainly consisting of empty shells; *A. chiroancanthus* showed a negative correlation. The pattern of distribution was studied by using the coefficient of dispersion. *G. intermedia* and *P. longicornis* were contagiously distributed; the other species occurred in too low numbers for the results to be valid. *G. intermedia* lived c. 1 year, and the larvae settled from Aug. to Nov. 0.002% were infected by *Lernaeodiscus galatheae. P. longicornis* reached an age of c. 2 years (some probably 3) and reproduced the first. The larvae settled mostly in Aug. and Sept. *P. bernhardus*, older than c. 1 year, probably migrated to deeper water. 2.1% were infected by *Peltogaster paguri. P. cuanensis* lived at least 2 years; few reproduced the first. One brood a year is probable. 1.3% were infected by *Athelges paguri*, 2.0% by *P. paguri*, 5.5% by *Peltogaster curvatus*, and 1.7% by *Gemmosaccus sulcatus*. Young *P. prideauxi* occurred in shallow water when the temperature exceeded 8—10°C. A commensal polychaete, *Iphitime paguri*, new to the Norwegian fauna, was found. *A. chiroacanthus* lived c. 2 years and reproduced the first. One brood a year occurred. 0.7% were infected by *P. paguri* and 0.5% by *G. sulcatus*. Selection of shells by the pagurids has been discussed. *Labrus berggylta* was the main predator.

CONTENTS

INTRODUCTION

Several investigators have studied the European species of Anomura, but none has been specially interested in the biology of sympatric species as ALLEN (1966) has been in the species of Caridea found off the northeast coast of England.

Contribution from the Biological Station of the University of Bergen, Espegrend, N-5065 Blomsterdalen, Norway.

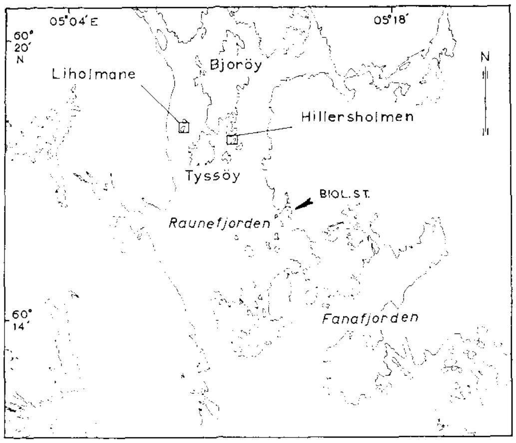

Fig. 1. Raunefjorden and the two localities investigated.

The aim of this investigation[1] was to study the biology of populations of Anomura from a restricted area. Two shallow sounds were chosen as localities which were inhabited by one species of the family Galatheidae, one species of Porcellanidae and four species of Paguridae. The investigation was carried out over a period of 18 months.

From the same localities JENSEN (unpubl.) has studied the echinoderms and HÖISÆTER (1968 and unpubl.) the gastropods, partly during the same period.

TOPOGRAPHY AND BOTTOM TYPES

Raunefjorden, southwest of Bergen, is in its northern end divided into two branches by the islands Bjoröy and Tyssöy. The two localities investigated are situated one in each of these branches (Fig. 1). The first, here called Hillersholmen, lies between the islets Hillersholmen and Glomsnesskjæret at a depth of 7—9 m and covers an area of about 1,360 m^2 (Fig. 2). The second, here called Liholmane, is situated between the islets Liholmane and Kjelen at 7—8 m depth with a sampling area of about 800 m^2 (Fig. 3). The depth increases gradually at both ends of the two sounds.

At Hillersholmen three types of bottom were distinguished, at Liholmane only one (Figs. 2 and 3). The rectangles indicate the sampling areas, and the following terms[2] are used for description of the substrate: pebbles (64—16 mm), empty shells (>16 mm), shell gravel (16—2 mm), and shell sand (<2 mm).

Bottom type 1 (Fig. 4) lies towards Glomsnesskjæret and is bounded by the

[1] The present paper is an extract from my thesis for the Cand. real. degree (SAMUELSEN 1969) which is deposited in manuscript form at the University Library of the University of Bergen.

[2] As used at the Biological Station, Espegrend.

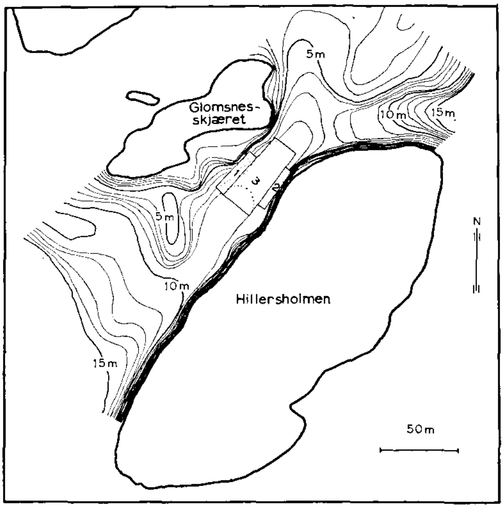

Fig. 2. Hillersholmen and the situation of bottom type 1, 2, and 3.

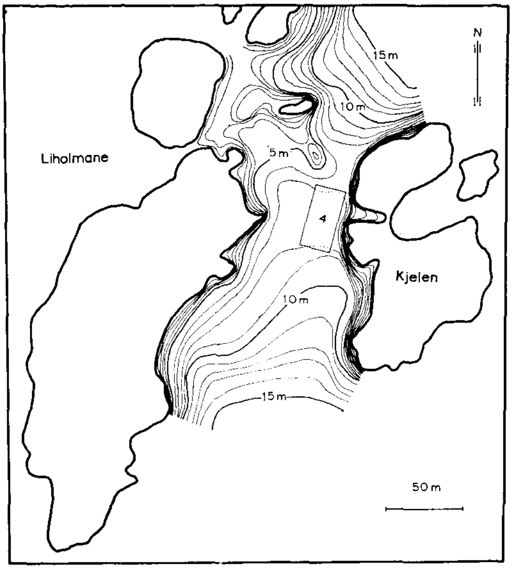

Fig. 3. Liholmane and the situation of bottom type 4.

islet and bottom type 3 and covers an area of approximately 30 m by 7 m. It consists mainly of shell sand and shell gravel with some empty shells.

Bottom type 2 (Fig. 5) is situated between Hillersholmen and bottom type 3. It covers an area of about 30 m by 5 m and consists mainly of shell gravel and empty shells of *Balanus*, *Lima*, *Modiolus*, and *Mytilus* with some pebbles. It is partly overgrown with *Pomatoceros triqueter* (L.).

Bottom type 3 (Fig. 6) lies between bottom type 1 and 2 and covers an area of approximately 50 m by 20 m. It consists mainly of empty shells of *Ensis* with some shell gravel and pebbles and is thickly overgrown with *P. triqueter.*

Bottom type 4 (Fig. 7) is situated between Liholmane and Kjelen and is bounded by fine shell sand and boulders. It covers an area of approximately 40 m by 20 m. Bottom type 4 is similar to bottom type 3, but more unevenly distributed and with a lower content of empty shells. In addition there are some more pebbles. There is less *P. triqueter* than on bottom type 3.

All four bottom types extend further than indicated by the sampling areas.

The volume of the coarse fraction, >16 mm, was determined on 20 1/4 m^2 samples of the substrate from bottom type 1, 20 from 2, 35 from 3, and 30 from bottom type 4. The means and standard deviations of the volume have been calculated for each bottom type (Fig. 8). The amount of coarse substrate increases through the bottom type 1, 2, and 3 at Hillersholmen, the three bottom types being distinctly different. Bottom type 4 at Liholmane is intermediate between 2 and 3, but more similar to bottom type 3 than to 2.

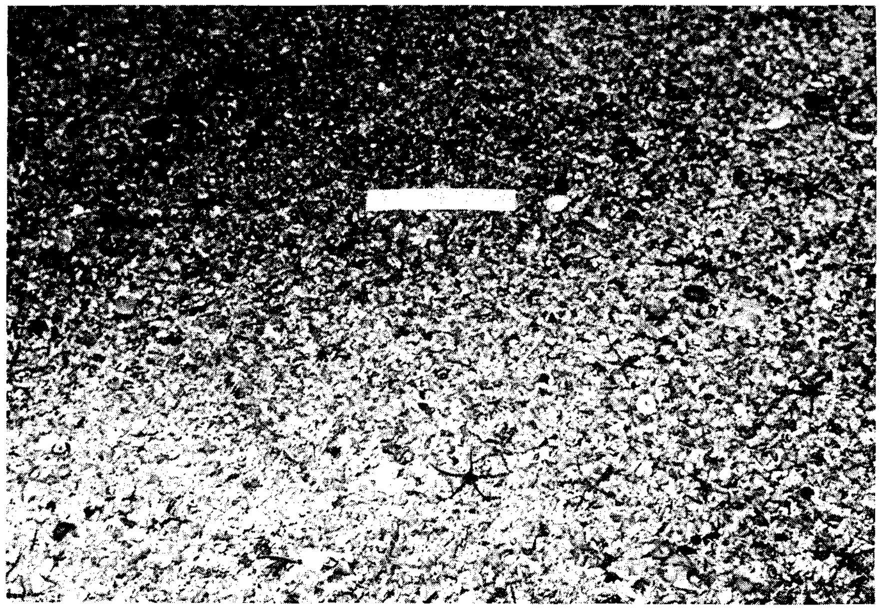

Fig. 4. Bottom type 1 at Hillersholmen (scale 10 cm).

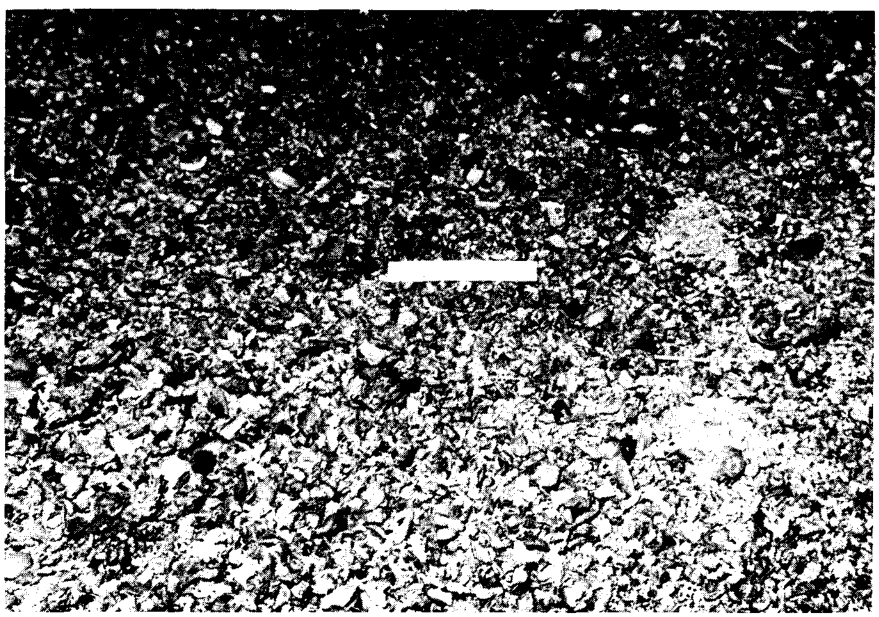

Fig. 5. Bottom type 2 at Hillersholmen (scale 10 cm).

The differences in coarseness of the substrate of the bottom types seem to be determined by the supply of dead shells and the sorting effect of the tidal currents running through the sounds (see p. 31). At Hillersholmen there is mainly a one

Fig. 6. Bottom type 3 at Hillersholmen (scale 10 cm).

Fig. 7. Bottom type 4 at Liholmane (scale 10 cm).

way current which corresponds in strength with the coarseness of the bottom types 1, 2, and 3. The current at Liholmane, above bottom type 4, alternates in direction and is weaker than the current above bottom type 3.

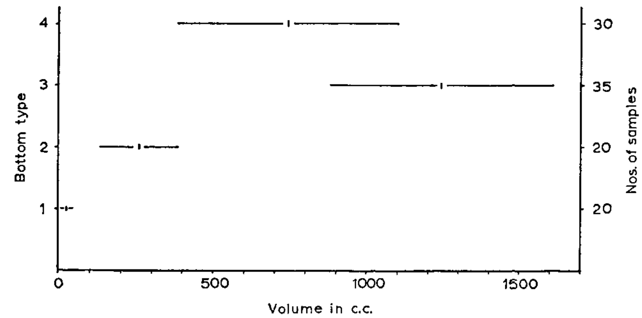

Fig. 8. Volume of the coarse fraction (> 16 mm) of 1/4 m² samples from the four bottom types. Means and standard deviations have been calculated.

MATERIAL AND METHODS

At Hillersholmen the material was collected from January 1967 to July 1968 and at Liholmane from February 1967 to July 1968 (except the current measurements 21 Sept. 1968 and 6 Feb. 1969). 39 hauls with a triangular dredge were taken on bottom type 3, and 2 hauls on bottom type 4. Quantitative samples were collected by diving. A frame (50 × 50 cm) was placed randomly on the bottom and animals and substrate were taken by hand and transferred to a plastic bag. The samples were taken about 7 cm down into the substrate to make sure none of the anomurans was left out. 20 samples of 1/4 m² were taken from bottom type 1, 21 from 2, 50 from 3, and 36 from bottom type 4.

All samples were sorted by hand in the laboratory. This was facilitated by using a fish poison, "Pro-noxfish" (MANNING 1960), which makes the animals move. They were thus easily seen. The animals were fixed and preserved in 80% alcohol and algae in 4% formaldehyde. The main part of the flora and fauna was identified to species.

The anomurans were counted, determined to sex (when secondary sexual characters were developed), and examined for eggs, parasites, and other associated flora and fauna. The carapace length of each specimen was measured as shown by PIKE (1947) and PROVENZANO (1959). Ten specimens of each species were randomly selected and the stomach contents examined.

Temperature and water samples were taken about 10 cm above the bottom at each locality by divers. The method of Knudsen and Winkler was used for derermination of S and O_2 respectively. Current measurements were done with subsurface drifters at 5 m depth between two fixed points (for details, see SAMUELSEN 1969).

Underwater photographs were taken with a Nikonos camera (U.W. Nikkor f=28 mm lens) and a Calypso Strobe, Model 211, electron flash.

HYDROGRAPHY

The variations in temperature and salinity are shown in Fig. 9. The temperature was about the same at both localities ranging from 4.1 °C to 16.6 °C. The variations in salinity did not deviate significantly between the localities; the most extreme variation, however, was from 32.83‰ to 24.09‰ at Hillersholmen.

At both localities the content of oxygen was always high with 79.8% saturation as lowest value measured (Jan. 1967, Hillersholmen).

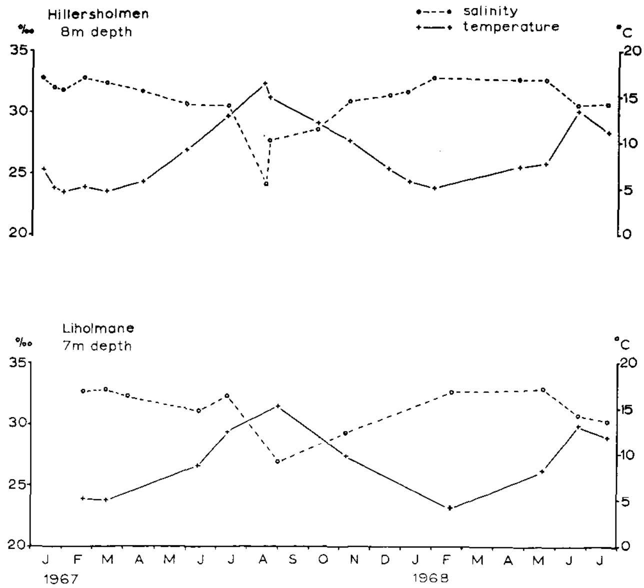

Fig. 9. Variations in the salinity and temperature at the sampling localities.

Current measurements were made at the two localities through two comparable tidal periods. At Hillersholmen the current ran in a northeasterly direction with the highest velocity (40.8 cm/sec) at LW and the lowest (3.8 cm/sec) at HW. This supports all my earlier observations of the current when diving, however, higher velocity (at least 2 knots, LW and SW wind) has been observed. When using three subsurface drifters at the same time I found that the highest velocity was in the middle of the sound (bottom type 3) and that there was a higher velocity at the Hillersholm side (bottom type 2) than at the Glomsnesskjær side (bottom type 1). On Liholmane (bottom type 4) the current ran towards north with the rising tide and south with the falling tide. Highest velocity (36.1 cm/sec) was measured when the current ran north (with S wind).

As regards temperature, salinity, and oxygen the two localities are very similar. The variations, with high temperature and low salinity during the summer and the opposite during the winter, are normal events in Norwegian fjords in shallow water. The currents, on the other hand, are different through the two sounds. At Hillersholmen a relatively strong current runs one way, while at Litholmane a weaker current alternates in direction with the tide.

FLORA AND FAUNA

15 species of algae and 205 species of animals were identified from the two localities. (A list of species is given in Samuelsen 1969.) With a few exceptions the species of Protozoa, Nematoda, and Copepoda were not identified. The actual number of species should thus be higher.

Table 1. Number of species found on the four bottom types.

Bottom type	1	2	3	4
Algae	5	6	12	14
Animals	92	115	176	138

The number of algal species increased through the bottom types 1, 2, 3, and 4 (Table 1). Bottom type 4 possessed in addition the largest number of specimens both summer and winter. The number of species in the fauna increased through the bottom types 1, 2, 4, and 3 (Table 1) and thus corresponded with the coarseness of the substrate.

In addition to *Pomatoceros triqueter*, which was used for description of the bottom types, I will mention some other characteristic species. The echinoderm data used are calculated from quantitative samples taken throughout a year (JENSEN pers. commn). *Ophiura albida* FORBES was conspicuous on bottom type 1 (see Fig. 4) with an average number of 21 specimens per 1/4 m^2 (2 specimens per 1/4 m^2 on bottom type 2, 1 on 3, and 4 on bottom type 4). *Spadella cephaloptera* (BUSCH), a chaetognat living on the bottom, was only found on this bottom type. A small nudibranch, *Embletonia pulchra* (ALDER & HANCOCK), was abundant too. *Modiolus modiolus* (L.) and *Lima hians* (GMELIN) were common on bottom type 2. *Strongylocentrotus droebachiensis* occurred with 14 specimens per 1/4 m^2 (2 specimens per 1/4 m^2 on bottom type 1, 5 on 3, and 4 on bottom type 4). On bottom type 3, *Ophiocomina nigra* (ABILDGAARD) was very common. An average number of 157 specimens per 1/4 m^2 was found (1 specimen per 1/4 m^2 on bottom type 1, 50 on 2, and 44 on bottom type 4). According to MORTENSEN (1924) this species prefers localities with strong currents. *Ophiopholis aculeata* (O. F. MÜLLER) was conspicuous too. The gastropod fauna was rich (HÖISÆTER 1968 and pers. commn). Pyramidellids, which are specifically associated with *P. triqueter*, were found in great numbers with a maximum for *Odostomia eulimoides* HANLEY with 2,027 specimens in a single 1/4 m^2 sample. Bottom type 4 can be characterised by the algae as most elements of the fauna found on the other bottom types were present here too, but in smaller quantities. The aglaozonia stage of the brown alga *Cutleria multifida* (Sm.) GREV. covered great parts of the substrate all the year round. This species was also found on the other bottom types, however not commonly. *Lithothamnion granii* FOSL. was abundant too, and during the summer the amount of *Monostroma fuscum* (POST. & RUPR.) WITTR. and *Desmarestia aculeata* (L.) LAMOUR were conspicuous.

NUMERICAL DISTRIBUTION OF THE ANOMURA

The following species were found at both localities: *Galathea intermedia* LILLJEBORG, *Pisidia longicornis* (L.), *Pagurus bernhardus* (L.), *P. cuanensis* THOMPSON, *P. prideauxi* LEACH, and *Anapagurus chiroacanthus* (LILLJEBORG). In addition one specimen of *Galathea squamifera* LEACH and one of *G. strigosa* (L.) was found at Hillersholmen, but as they normally occur in rock-strewn slopes (SAMUELSEN 1968) they will not be treated further.

The percentage of each species within each bottom type and the average number of specimens were calculated from all the 1/4 m^2 samples collected (Fig. 10). On bottom type 1 94.2% of the anomurans were pagurids, and *G. intermedia* was the only galatheoid represented. The pagurids also dominated on bottom type 2 with 65.0%. Both *G. intermedia* and *P. longicornis* occurred in equal abundance with 17.7% and 17.3% respectively. The galatheoids constituted 84.6% on bottom type 3 with 42.8% *G. intermedia* and 41.8% *P. longicornis*. *P. cuanensis* was the dominating pagurid here as on the other three bottom types. The galatheoids dominated on bottom type 4 with 65.3%. There were 49.6% *G. intermedia* and 15.5% *P. longicornis.*

Both *G. intermedia* and *P. longicornis* increased in number through the bottom types 1, 2, 4, and 3. They were thus positively correlated with the amount of coarse substrate. *A. chiroacanthus* showed a negative correlation giving the highest number of specimens on bottom type 1. The other pagurids showed no such correlation; however, *P. bernhardus*, most common on bottom type 4 at Liholmane, decreased in number through bottom type 1, 2, and 3 at Hillersholmen. *P. cuanensis* was most common on bottom type 2, *P. prideauxi* on bottom type 3.

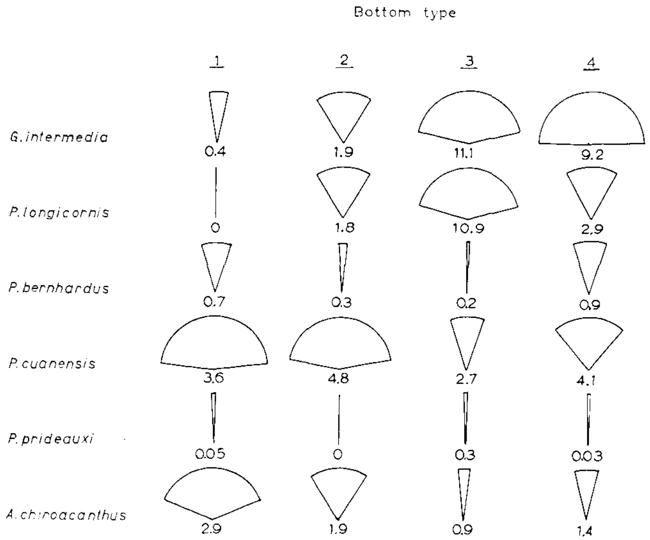

Fig. 10. Percentage of the six species on each of the bottom types (100% = 360°). Below the sectors; average number of specimens per 1/4 m^2.

Bottom type	1	2	3
2	2231		
3	1343	2255	
4	2943	2550	4437

Fig. 11. "Trellis diagram" showing the degree of similarity between the anomuran fauna from the four bottom types.

Three of the species, *G. intermedia*, *P. longicornis*, and *P. prideauxi* varied in density through the year. The average number of *G. intermedia*, collected on bottom type 3 from January to May 1967, was 16 per 1/4 m². No samples were taken in June. In July the density had decreased, and the average number of specimens from July up to and including October was 4 per 1/4 m². In November the density increased, and the average number up to and including June 1968 was 14 per 1/4 m². The next month there were only 6 specimens per 1/4 m². Similar events occurred on bottom type 4, but the decrease in density was in June both years. *P. longicornis* showed less regular fluctuations than *G. intermedia*. On bottom type 3 the average number of specimens was 15 per 1/4 m² in January and February 1967. From March until December the density was low with 6 specimens per 1/4 m² on the average. From December to June 1968 the average was 18 specimens per 1/4 m², and in July only 9. *P. prideauxi* was caught only sporadically when the quantitative method was used. This is explained by the fact that the comparatively fast moving *P. prideauxi* escaped the sampling quadrate. When using the triangular dredge *P. prideauxi* was frequently taken from July to December 1967. This species, which I have otherwise collected from deeper water all the year round, thus occurred in shallow water when the temperature was higher than 8–10 °C.

The degree of similarity between the bottom types was calculated using the relative density of the anomuran species (GREIG-SMITH 1964). On Hillersholmen the greatest similarity was found between bottom type 2 and 3 which are adjacent (Fig. 11). Nearly the same value was found between bottom type 1 and 2 on each side of bottom type 3. There was least accordance between the adjacent bottom types 1 and 3. The anomuran fauna on all the bottom types at Hillersholmen were more similar to that on bottom type 4 at Liholmane than to each other, the highest degree of similarity being between bottom type 3 and 4.

If the bottom types, expressed by the amount of coarse substrate (Fig. 8), affect the composition of the anomuran fauna, bottom type 1 should resemble bottom type 2 more than the others, 2 should resemble 4, and 4 should resemble 3. This was the case except for bottom type 1 which was more similar to 4 than to 2, however the deviation may be explained by the composition of the substrate. Bottom type 4, which was very similar to bottom type 3, possessed small patches of shell sand among the coarser material, not unlike the substrate found on bottom type 1. Bottom types 2 and 1 had no such features in common. I therefore conclude that the composition of the anomuran fauna at Hillersholmen and Liholmane is determined by the bottom type.

The pattern of distribution was studied by using the coefficent of dispersion

$$\frac{S_x^2}{\bar{x}} = \frac{(x - \bar{x})^2}{\bar{x}(n-1)}$$

which is equal to unity in a randomly dispersed population, <1 if the distribution is more even than random (regular distribution), and >1 if there is a tendency to aggregation (contagious distribution) (GREIG-SMITH 1964). The difference between the calculated ratio and unity was compared with its standard error by a *t* test. This test was applied to two series of 10 (ser. 1) and 6 (ser. 2) samples of 1/4 m² collected 21 August 1967 and 24 June 1968 respectively, both from bottom type 3 at Hillersholmen. *P. prideauxi* was not present in either of the series. *P. bernhardus* was excluded as only one specimen occurred in each series. *G. intermedia* and *P. longicornis* showed a contagious distribution at the 0.1% level (Table 2); the distribution of *P. cuanensis* was not significantly different from random; the apparently regular distribution of *A. chiroacanthus* was not significant either.

Table 2. Mean and coefficient of dispersion of *Galathea intermedia* (G. i.), *Pisidia longicornis* (P. l.), *Pagurus cuanensis* (P. c.), and *Anapagurus chiroacanthus* (A. c.) with the results of the significance test.

	G. i.	P. l.	P. c.	A.c.	Series
Mean nos. per 1/4 m²	3.0	6.5	1.9	0.3	1
	16.6	12.8	3.5	1.5	2
Coefficient of dispersion	3.407	5.237	1.690	0.777	1
	2.273	8.213	0.540	0.200	2
Probability	>0.001	>0.001	0.2—0.1	0.5—0.4	1
	0.1—0.05	>0.001	0.5—0.4	0.3—0.2	2

The coefficient of dispersion, which has been repeatedly used for benthos studies (HOLME 1964), has its disadvantages. URSIN (1960) has pointed out that the observed deviation from random distribution is dependent upon the mean in such way that low means always result in values near unity, and JONES (1961) has shown that the method is not satisfactory when the mean is less than 5 as was the case of *P. cuanensis* and *A. chiroacanthus*.

THE INVESTIGATED SPECIES

Galathea intermedia LILLJEBORG

At both localities *G. intermedia* revealed an affinity to the coarse substrate mainly consisting of empty shells and some pebbles. According to ALLEN (1967) the species is fairly common on rock, stones, gravel, and hard mud and sand, however no specimens were found on the adjacent rock and stones at the localities investigated. *In situ* I observed *G. intermedia* partly on, and partly between, the pieces of substrate. When disturbed the animal swam backwards hiding itself in small cavities formed by the empty shells. Though all the *Galathea* species are active swimmers (ZIMMERMANN 1913), this species seldom succeeded in escaping when the substrate was collected.

The stomach contents consisted mainly of unidentifiable detritus with fine sand, silicious spicules, foraminiferans, radiolarians, and small parts of crustaceans. Observations in an aquarium showed that *G. intermedia* fed by two methods. Large pieces of food (e.g. shell meat) were taken by the chelae and maxillipeds and passed to the mandibles. More usually the third maxilliped was used to collect finely divided material from the substrate. *G. intermedia* thus showed a similar feeding habit to that of *G. squamifera, G. strigosa*, and *G. dispersa* studied by NICOL (1933).

For studying growth and reproduction all the specimens from both localities were combined as no significant differences could be found (SAMUELSEN 1969). (The same is considered true for the other species investigated.) Fig. 12. shows the size frequency histogram of *G. intermedia*. Of 1,420 specimens collected there were 3 juveniles, 666 ♂♂, and 751 ♀♀. The ♀♀ were more numerous throughout the whole period. Small specimens, with lengths from 2.05 mm to 2.45 mm, found from August to January, represent recently settled animals which, according to SARS (1889), should be about this size. Few specimens measured more than 6.6 mm and the largest was an ovigerous ♀ which was 7.6 mm long. The mean length of *G. intermedia* in October 1967 was 3.63 mm and in May 1968 5.06 mm. In seven months the average growth thus was 1.43 mm. The ♀♀ seem to grow faster than the ♂♂ as the mean length of ♀♀ and ♂♂ in May 1968 was 5.21 mm and 4.84 mm respectively. After reaching a length of about 5 mm the rate of growth seems to decrease in the same fashion as shown for *G. squamifera* by PIKE (1947).

Ovigerous ♀♀ were found from the middle of March (1967 and 1968) to the beginning of October (1967). Large ♀♀ carried eggs earlier, and in a greater number, than smaller ♀♀. The smallest ♀ with eggs measured 3.6 mm. The size of the egg increased from c. 0.4 mm when freshly laid to c. 0.5 mm before hatching. In October all eggs were ready to hatch. Eggs in March and juveniles in August indicate a time of development of about 5 months.

The growth of *G. intermedia* seems to be sufficiently rapid for larvae, settling during the autumn and even early winter, to reproduce the following breeding season. The unimodal size distribution, combined with a decrease in number of specimens during the summer, points towards a lifespan of about one year. Some specimens probably survive into the second year and reproduce once more.

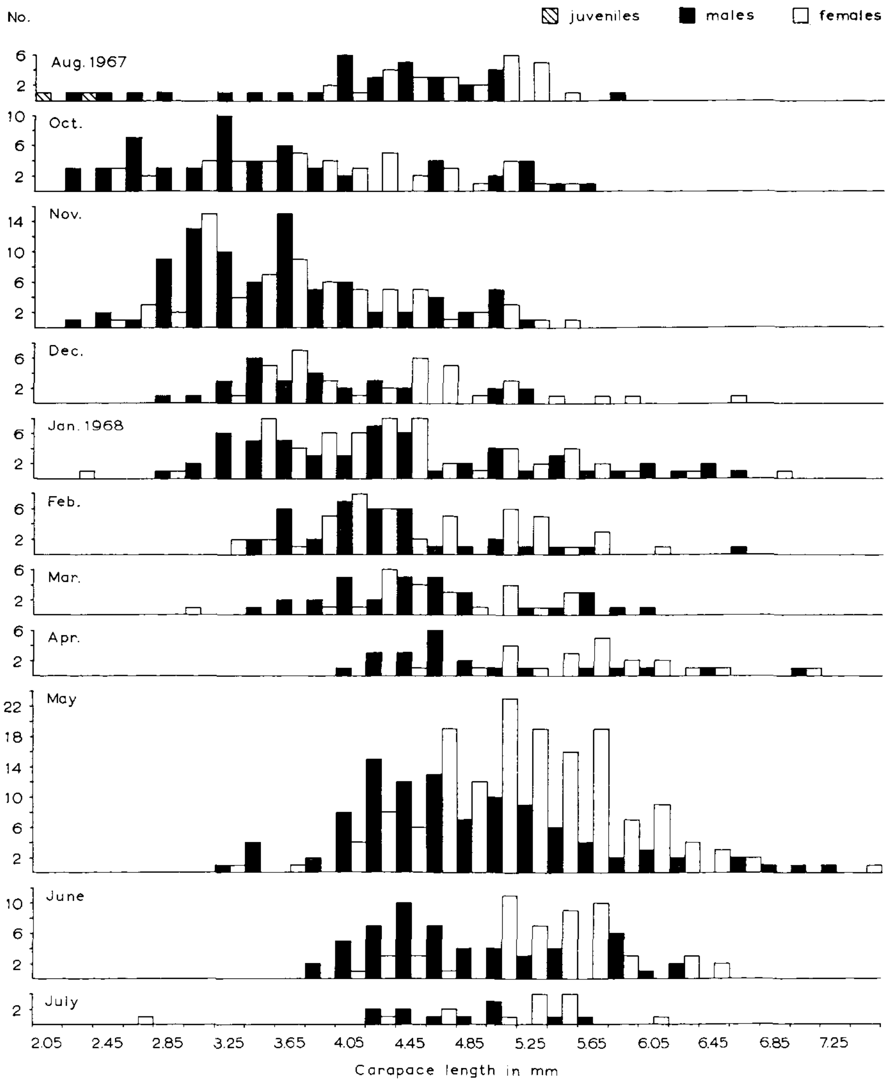

Fig. 12. Size distribution of *Galathea intermedia* from Hillersholmen and Liholmane for the period Aug. 1967—July 1968. The earlier months of 1967 are not included, since low numbers were obtained which repeated the pattern shown in the corresponding period in 1968.

Pisidia longicornis (L.)

This species was mainly found in the coarse substrate where empty shells, in thick layers, made small cavities where the animals were hiding. *P. longicornis* was never observed on the surface of the substrate. Elsewhere I have found it under stones on rocks (SAMUELSEN 1968), in hapters of *Laminaria*, and in lumps of the serpulid polychaet, *Filigrana implexa* BERKELEY, which also shows the hiding habit of this species. When picking up an empty shell I very often observed *P. longicornis* on the underside, camouflaged by its colour and pattern. If I turned the shell upside down, and in some cases irritated the animal, it crawled rapidly to the opposite side. The species is able to swim, but did so only if it was strongly irritated.

The feeding habit has been studied by NICOL (1933). The species is mainly a suspension-feeder and collects fine particles with the long, hairy third maxillipeds. In the stomachs I only found undefined detritus. Acording to NICOL (op. cit.) the stomach contents are much more finely divided than those of the *Galathea* species, and are closely comparable to those of the filter-feeding polychaets and molluscs.

Of 1,041 specimens collected there were 3 juveniles, 538 ♂♂, and 500 ♀♀. The size distribution is shown in Fig. 13. One juvenile found in August, and one in October, were in the megalopa stage and measured 1.4 mm and 1.5 mm respectively. Few specimens measured more than 6.0 mm, and the largest was a 6.8 mm long ♂. My specimens are thus smaller than those mentioned by SELBIE (1914). *P. longicornis* from Raunefjorden showed mainly a bimodal size distribution. The mean length of the smallest group increased from 2.10 mm in October 1967 to 3.29 mm in June 1968 which gives an average growth of about 1.2 mm in eight months. The mean length of the larger animals from May and June 1968 indicates a further average growth of about 1.7 mm in one year. The smallest animals had a rapid growth, probably from August to November. Then a stagnation seemed to occur which lasted to May when a rapid growth started again. Both ♂♂ and ♀♀ seemed to have similar growth rates.

From May (1967 and 1968) to October (1967) I found ovigerous ♀♀. Some of the eggs were ready to hatch in the middle of June, all in August and October (no samples from Sept.). Larger ♀♀ had earlier and more eggs than smaller ♀♀. The smallest ♀ carried 4 eggs and was 3.3 mm long. The size of the eggs increased from c. 0.4 mm, early eggs, to c. 0.5 mm before hatching. From the size of the megalopa, and the young animals (in Oct.), it seems likely that most of the larvae settled in August—September. The time of development should thus be about 3—4 months.

The growth of the young specimens, settled during the autumn, should enable at least some of them to reproduce the next year. Most of the animals seem to live about two years, while a few reach an age of three years.

Three sessile species were found fastened onto *P. longicornis*. A foraminiferan, *Cibicides lobatulus* (WALKER & JAKOB), was common from April to August. This species was mainly attached to carapace and chelipeds where I also found *Spirorbis spirillum* (L.) and *Callopora lineata* (L.); the latter is a bryozoan earlier reported from *P. longicornis* (MARCUS 1940).

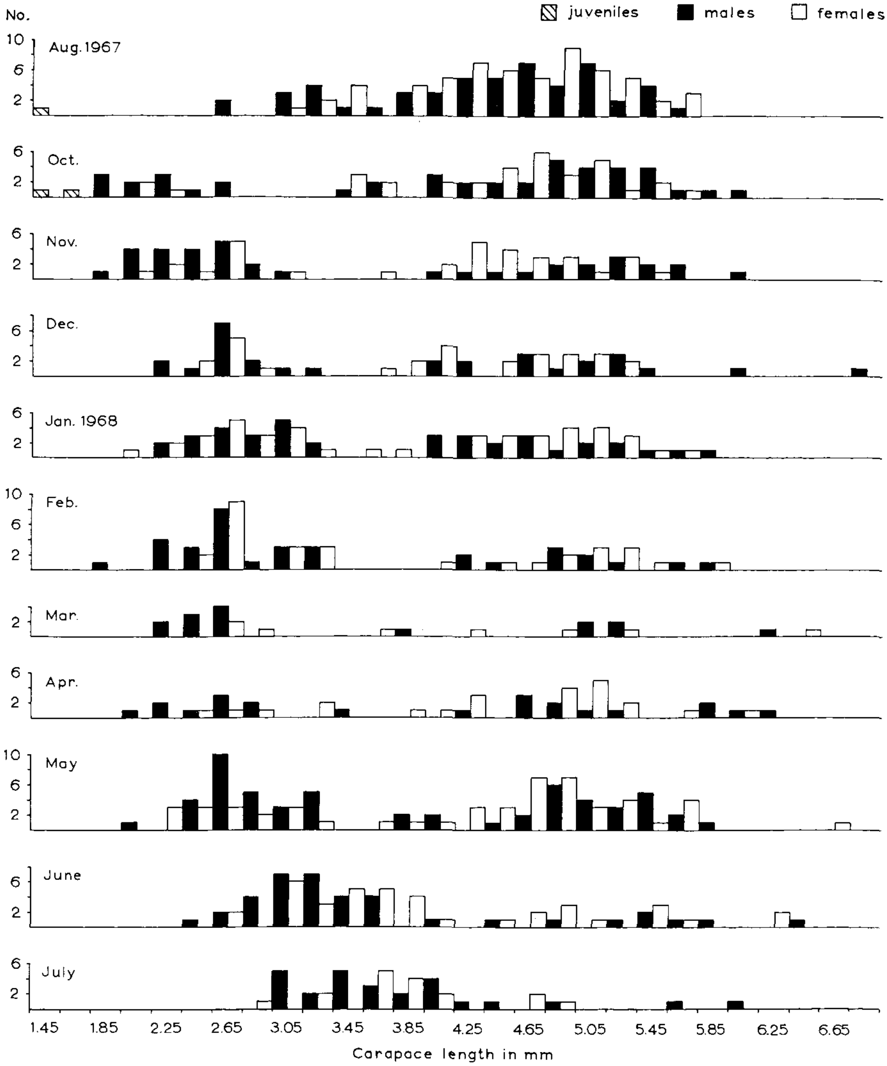

Fig. 13. Size distribution of *Pisidia longicornis* from Hillersholmen and Liholmane for the period Aug. 1967—July 1968. The earlier months of 1967 are not included, since low numbers were obtained which repeated the pattern shown in the corresponding period in 1968.

Pagurus bernhardus (L.)

P. bernhardus was found in small numbers on all the four bottom types. Elsewhere in the area I have observed this species on almost all kinds of bottoms. At both localities it crawled upon the substrate, but also occurred buried in shell sand so that its shell was partly covered. When disturbed, the animal normally tried to escape. In samples taken by the dredge I often observed that *P. bernhardus* left its shell, especially if remaining without seawater for some time.

ORTON (1927) has studied the mode of feeding. *P. bernhardus* obtained food largely by its small, left cheliped and third maxillipeds. Larger pieces of food (e.g. shell meat) were torn by both chelipeds and passed to the mouth. In an aquarium I have observed that *P. cuanensis*, *P. prideauxi*, and *Anapagurus chiroacanthus* feed in a similar way. The stomach contents of *P. bernhardus* revealed detritus with sand grains, bits of algae and algal threads, foraminiferans, setae of polychaets, small gastropods, and bivalves together with parts of small crustaceans.

Of 277 specimens collected there were 2 juveniles, 149 ♂♂, and 126 ♀♀. Because of the very low number of specimens found each month, no histogram showing the sizes was made. The smallest specimens were collected in October 1967 and measured from 1.3 mm to 1.6 mm. They thus corresponded in size with the first, young hermit stage mentioned by JACKSON (1913) and PIKE & WILLIAMSON (1959). The mean length of all the specimens was 5.67 mm, and the largest was a ♂ which measured 11.0 mm. According to PIKE (1961) *P. bernhardus*, which can reach an age of at least three years, has a modal size of 7—9 mm, with a maximum length of c. 13 mm, in the one-year group. At Hillersholmen and Liholmane the animals should thus be at most one year old. Later they probably migrate to deeper water at the ends of the sounds where I frequently have found specimens measuring more than 20 mm.

Ovigerous ♀♀ were collected from January to July both years. The smallest ♀ with eggs measured 4.8 mm and had few eggs compared with larger specimens. The size of the eggs ranged from c. 0.5 mm for early eggs to c. 0.7 mm before hatching. The eggs are thus smaller than those reported by MACDONALD, PIKE & WILLIAMSON (1957). The larvae occurred in Raunefjorden and Fanafjorden from March to the end of October, with a maximum in July (SANKARANKUTTY pers. commn). From the British Isles, PIKE & WILLIAMSON (1959) found that the incubation period of the eggs probably lasted about 3 months. If this is valid for the Raunefjord specimens, the occurrence of larvae indicates a total time of development of 5 to 6 months. *P. bernhardus*, which can reproduce in its first year, thus reproduces once a year during the spring. This is also suggested by PIKE & WILLIAMSON (op. cit.).

Nearly all the shells inhabited by *P. bernhardus* were more or less covered with epibiotic growths consisting of algal threads, *Cibicides lobatulus*, *Hydractinia echinata* (FLEMING), *Gonactinia prolifera* (SARS), *Pomatoceros triqueter*, *Hydroides norvegica* (GUNNERUS), *Spirorbis spirillum*, *S. pagenstecheri* QUATREFAGES, *S. borealis* DAUDIN, *S. tridentatus* (LEWINSEN), *Monia patelliformis* (L.), *Celleporella hyalinina* (L.), and *Flustrella hispida* (FABRICIUS). The serpulid polychaets were most abundant. Burrowing in the shell were *Cliona* sp., *Polydora* sp., and *Hiatella arctica* (L.). Inside the aperture I found, in some shells, *S. spirillum* and *Callopora lineata*. *Polydora* sp. was found inside the shell too, behind the hermit crab, lying in the upper whorls as described for *P. commensalis* ANDREWS (ANDREWS 1891).

Pagurus cuanensis THOMPSON

This species avoided to a certain degree the coarsest substrate. In addition to bottoms with empty shells, shell gravel, and shell sand *P. cuanensis* is found on mud, sand, and gravel (ALLEN 1967). *In situ* the hermit crab sat in between the pieces of substrate or in small concavities on the surface or partly buried in the shell sand. *P. cuanensis*, which is a very hairy species, was usually covered with detritus on the visible parts of the animal. The shells were covered with epibiotic growths or detritus. This, together with slow movements, made *P. cuanensis* not easily seen. If the animal was disturbed it usually withdrew into the shell.

The stomach contents of this species consisted mainly of detritus with small mineral grains together with foraminiferans and polychaet setae.

Of 787 specimens examined 43 were juveniles, 389 ♂♂, and 355 ♀♀. A size frequency histogram is showed in Fig. 14. The juveniles, which had a mean length of 1.55 mm, were found in greatest numbers from October to January, but also occurred from January to May. Few specimens measured more than 5.5 mm; the largst was a 7.9 mm long ♂. Though not obvious, the size distribution seems to be mainly bimodal with an indication of a third group. This points towards a lifespan of at least two years. However, it is also possible that specimens, which would represent an evident third year group, may have migrated from the habitat. If specimens measuring from 1.85 mm to 3.45 mm and from 3.85 mm to 5.25 mm in June 1968 are said to each represent one year group, the means of 2.40 mm and 3.55 mm respectively indicate a growth of 1.15 mm in one year. A length of 2.4 mm will probably be reached about 8 months after the larvae have settled.

Ovigerous ♀♀ occurred from March (1967 and 1968) to August (1967). The smallest ♀ with eggs measured 3.5 mm which indicates that only a few of the animals settled the previous year would reach maturity in the following year. The eggs from both July and August were ready to hatch and measured c. 0.8 mm. Newly laid eggs were about 0.5 mm. The eggs are thus somewhat smaller than reported by MACDONALD, PIKE & WILLIAMSON (1957) for British waters. Few larvae were caught in Raunefjorden and Fanafjorden from July to October (SANKARANKUTTY pers. commn). MACDONALD, PIKE & WILLIAMSON (op. cit.) suggested that *P. cuanensis* reproduces twice a year, however; in Raunefjorden only one brood seems to occur.

Amongst epibionts was a brown alga, *Ectocarpus* sp., found attached to the antennae and the front of the carapace of one specimen. In addition *Cibicides lobatulus* was found on the carapace of several specimens. This foraminifer occurred frequently on the shells where I also found algal threads, *Hydractinia echinata, Gonactinia prolifera, Pomatoceros triqueter, Hydroides norvegica, Spirorbis spirillum, S. pagenstecheri, S. tridentatus, S. vitreus* FABRICIUS, *Acmaea virginea* (MÜLLER), *Monia patelliformis*, and *Lichenopora verrucaria* (FABRICIUS). These species were more or less the same as those found on shells occupied by *P. bernhardus*; the shells of *P. cuanensis*, however, were more frequently covered with algal threads and

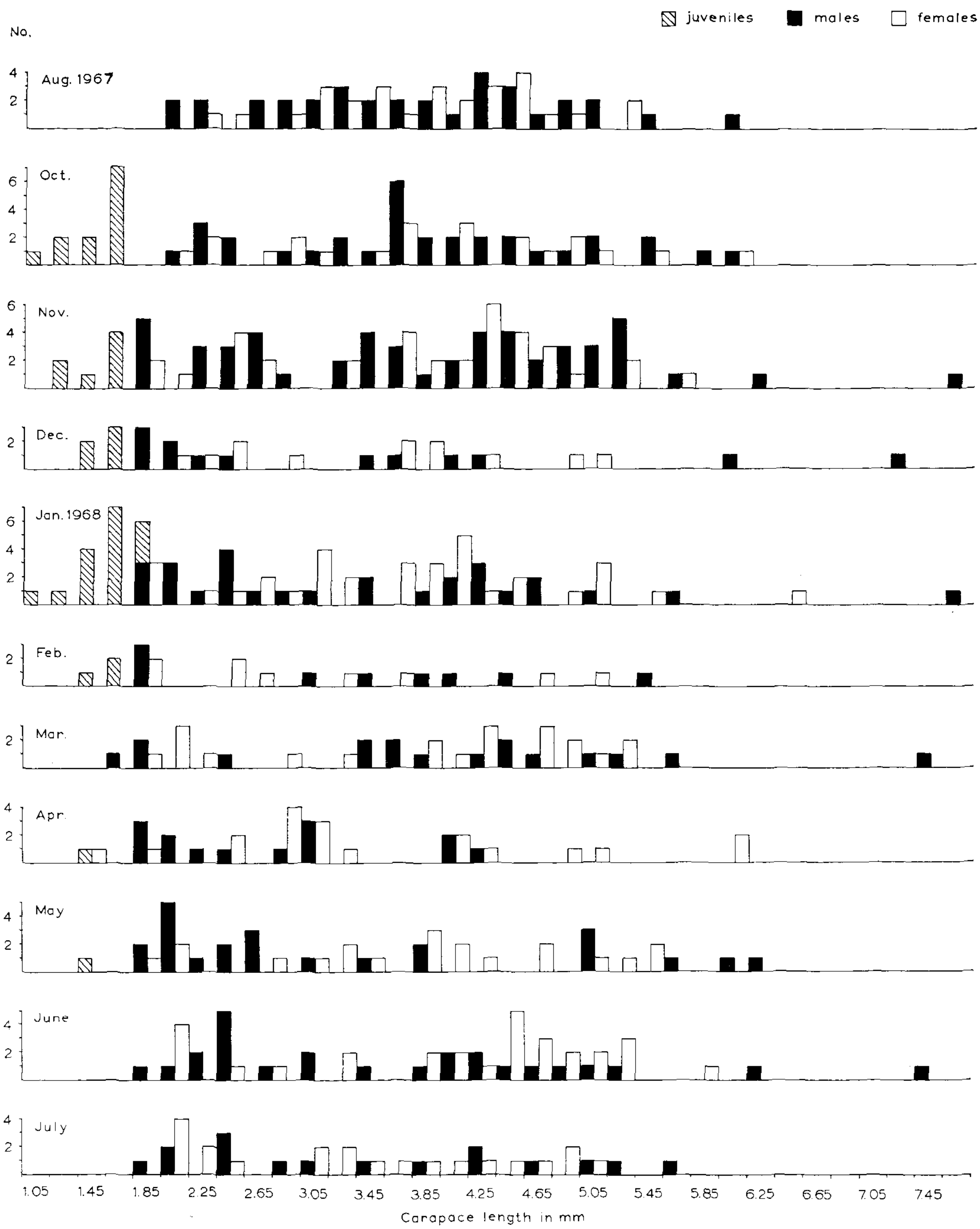

Fig. 14. Size distribution of *Pagurus cuanensis* from Hillersholmen and Liholmane for the period Aug. 1967—July 1968. The earlier months of 1967 are not included, since low numbers were obtained which repeated the pattern shown in the corresponding period in 1968.

detritus. *Cliona* sp., *Polydora* sp., and *Hiatella arctica* were found burrowing in the shell as for *P. bernhardus*, and *Spirorbis spirillum* was found attached inside the aperture. In the upper whorls, behind the hermit crab, the following species were observed: *Eulalia viridis* (O. F. MÜLLER), *Nereimyra punctata* (O. F. MÜLLER), *Nereis pelagica* (L.), *Ephesia gracilis* RATHKE, and *Polydora* sp., all polychaets, furthermore a harpacticid, *Thalestris gibba* (KRÖYER), and an amphipod, *Corophium bonelli* G. O. SARS. All the species occurred elsewhere at the localities as well. They can thus not be classified as commensales or symbionts without further investigation.

Pagurus prideauxi (LEACH)

Few specimens were collected. At the ends of the sounds, from 15 m to 30 m on shell gravel and shell sand, *P. prideauxi* was abundant, especially during the summer. The species has also been found on mud, muddy sand, and clean gravel and sand (ALLEN 1967, PIKE & WILLIAMSON 1959). *In situ* I have often observed *P. prideauxi* buried in shell sand so that the whole shell with the sea anemone, *Adamsia palliata* (BOHADSCH), has been covered. If disturbed, the hermit crab moved quickly backwards, partly with long jumps.

The stomach contents were similar that of *P. bernhardus*, with some more pieces of algae. HUNT (1925) made no distinction between these species as regards the food.

The 52 specimens collected consisted of 25 ♂♂ and 27 ♀♀. The mean length was 10.81 mm with two ♂♂ measuring 15.2 mm and 2.4 mm as maximum and minimum. PIKE (1961) estimated that specimens which measured c. 10 mm were one year old, and that a few ♂♂ survived into a third year, reaching a length of c. 23 mm. On deeper water in Raunefjorden I have collected several specimens with lengths from 15 mm to 20 mm, which indicates that only younger specimens occurred in shallow water at Hillersholmen and Liholmane when the temperature exceeded 8—10 °C.

Ovigerous ♀♀ were found from July to November 1967, however, no ♀♀ were in the samples from the other months. The larvae occurred in Raunefjorden and Fanafjorden in January, March, April, and from July to December with a maximum in August (SANKARANKUTTY pers. commn). This points towards two broods a year as PIKE & WILLIAMSON (1959) have shown. The size of the eggs ranged from c. 0.7 mm to 0.9 mm, which is in accordance with the measurements given by MACDONALD, PIKE & WILLIAMSON (1957). The smallest ♀ with eggs was 7.6 mm long.

Three specimens of *Iphitime paguri* FAGE & LEGENDRE were found associated with *P. prideauxi*. This polychaet has been described as a commensal to *P. bernhardus* by FAGE & LEGENDRE (1933). More recently the species has been reported from *P. prideauxi* (MARINE BIOLOGICAL ASSOCIATION 1957). It was pointed out in this book that morphological differences exist between the specimens from *P. prideauxi* and the specimens originally described. Similar differences were found on my specimens of which one lay across the carapace in the cervical suture and the other two in the upper whorls of the shell behind the hermit crab. Several *Iphitime paguri* have later been collected from deeper water in the Bergen area for further investigation (HÖISÆTER & SAMUELSEN unpubl.).

Specimens of *Polydora* sp. were observed inside the shell, and burrowing in the shell as in the case of the other *Pagurus* species. On the outer parts of the shell, not covered by *Adamsia palliata*, I found *Cibicides lobatulus*, *Hydroides norvegica*, and *Spirorbis spirillum*.

Anapagurus chiroacanthus (LILLJEBORG)

This species preferred mainly shell sand. It has also been found on sand, gravel, and muddy sand (ALLEN 1967, BOURDON 1965). *A. chiroacanthus*, which is the smallest pagurid in the Norwegian waters, was not easily seen *in situ*, mainly because of the small size, but also because it often occurred slightly buried in shell sand. In addition the species often possesses detritus on its hairs, but to a lesser degree than was the case with *P. cuanensis*. When disturbed, *A. chiroacanthus* usually withdrew into the shell.

The stomach contents revealed detritus with mineral grains, silicious spicules, foraminiferans, and radiolarians, similar to those of *G. intermedia*, but with a greater amount of detritus.

Of 409 specimens collected there were 1 juvenile, 200 ♂♂, and 208 ♀♀. The size distribution is shown in Fig. 15. The smallest specimens, found in October, November, January, and February, which measured from 0.8 mm to 1.1 mm, possibly represent the first young hermit stage, to judge by the size of the glaucothoe stage given by MACDONALD, PIKE & WILLIAMSON (1957). Few specimens were longer than 3.85 mm, the largest was a ♂ which measured 4.5 mm. BOUVIER (1940) gave lengths from 3 mm to 6 mm, while PIKE & WILLIAMSON (1959) regarded specimens from 3 mm to 4 mm as large animals.

Ovigerous ♀♀ were observed from April (1967 and 1968) to October (1967). The smallest ovigerous ♀ measured 1.5 mm and carried 15 eggs, while a 2.4 mm long ♀ had 30 eggs. Larger ♀♀ had still more eggs. Early eggs measured c. 0.4 mm, and those ready to hatch c. 0.6 mm. These sizes are thus in accordance with the measurements given by PIKE & WILLIAMSON (1959). The larvae were found in Raunefjorden and Fanafjorden from July to November with a maximum in August (SANKARANKUTTY pers. commn).

The size distribution seems to be bimodal despite the low numbers of specimens collected each month (Fig. 15). It is therefore possible that *A. chiroacanthus* lives about two years and reaches an average length of 3.30 mm (July 1967, largest group). The length of the smallest ovigerous ♀♀ indicates that young specimens settled during the autumn can reproduce the next summer. It seems reasonable that most of the ♀♀ carry eggs once a year.

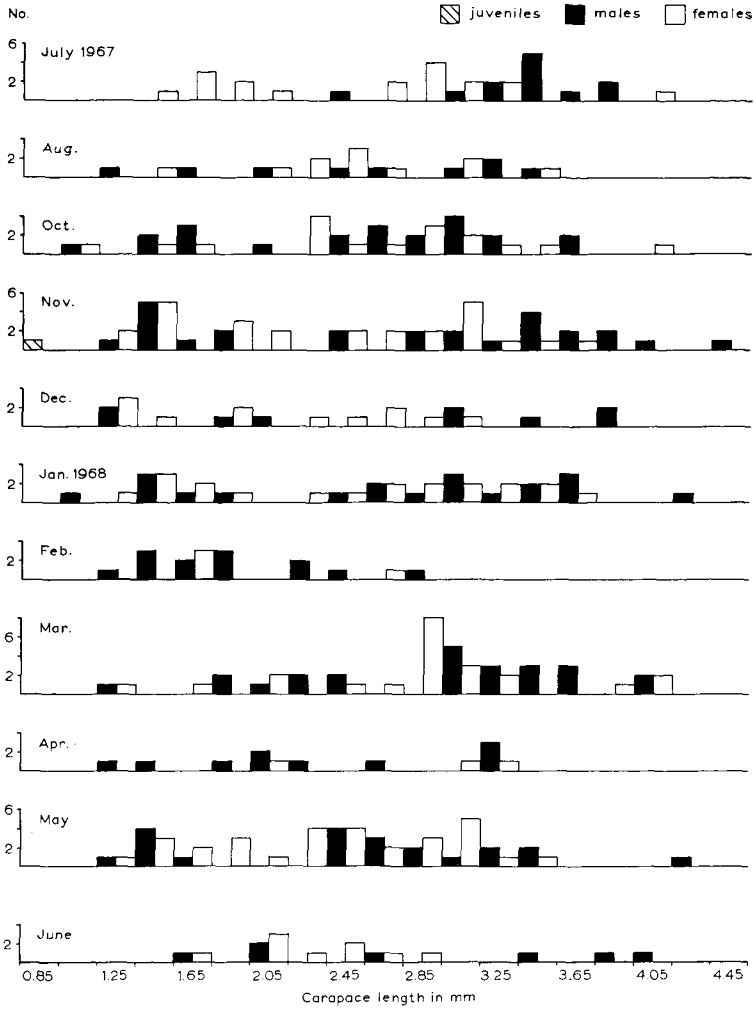

Fig. 15. Size distribution of *Anapagurus chiroacanthus* from Hillersholmen and Liholmane for the period July 1967—June 1968. The earlier months of 1967 are not included, since low numbers were obtained which repeated the pattern shown in the corresponding period in 1968.

The epibionts found on the shells consisted of *Cibicides lobatulus*, *Hydractinia echinata*, *Gonactinia prolifera*, *Pomatoceros triqueter*, *Hydroides norvegica*, and *Spirorbis tridentatus*. The polychaets were most common. Inside the shell behind the hermit crab, *Corophium bonelli* was observed as was the case of *P. cuanensis*.

SELECTION OF SHELL

The four species of pagurids were examined for shell preference. However, in the preserved material several specimens of *P. bernhardus*, *P. cuanensis*, and *A.*

Table 3. Number of *Pagurus bernhardus*, *Pagurus cuanensis*, and *Anapagurus chiroacanthus* with and without shell from Hillersholmen (H) and Liholmane (L).

Species	Locality	Nos. with shell	Nos. without shell
P. bernhardus	H	168	70 (29.4%)
	L	36	3 (7.7%)
P. cuanensis	H	481	96 (16.6%)
	L	164	46 (21.6%)
A. chiroacanthus	H	234	102 (30.4%)
	L	39	34 (46.6%)

chiroacanthus were found without shells (Table 3). For *P. bernhardus* the loss of shell is due to the treatment of the sample; *P. bernhardus* frequently left its shell when roughly treated (see p. 39) and none were observed *in situ* without shell. The difference in percentage of specimens without shell from Hillersholmen (24.9%) and Liholmane (7.7%) supports this, as *P. bernhardus* was mainly collected by dredge at Hillersholmen, and by hand at Liholmane. In the case of *P. cuanensis* and *A. chiroacanthus* the lack of shell can not be explained solely by the treatment of the samples. *In situ* I have observed both species without shell hiding in concavities on the substrate and in tufts of dead *Desmarestia*. In both cases the whole body of these hairy species was covered with detritus and thus not easily seen. At Liholmane there were 5.3% more *P. cuanenis* without shells than at Hillersholmen, and of *A. chiroacanthus* 16.2%.

In the laboratory 6 specimens of *P. cuanensis* without shells, collected from dead *Desmarestia* (Liholmane), were offered suitable shells. In the course of a few hours all the specimens possessed shells. Another experiment was carried out with 9 specimens of *P. cuanensis* with, and 9 specimens without shells, kept in separate glass tanks ($15 \times 10 \times 7$ cm), A and B respectively, with natural substrate. The animals lived in running seawater and were fed once a month with *Mytilus*. After 41 days all specimens were alive in tank A and 3 in B. Of the 6 dead specimens in B there was only remnants of one, on which the largest animal (5.1 mm) was eating. 56 days later all the specimens were alive in A, but in tank B only the largest specimen was left. The situation was the same 30 days later.

The experiments showed that animals without shells occupied accessible shells, and that the mortality (here probably due to cannibalism) among "naked" specimens was high. It should be noted that 9 specimens in the glass tank used, corresponded to about 150 specimens per 1/4 m^2, and 1 specimen to about 17, while the maximum density on the localities was 20 pagurids (several species) per 1/4 m^2. However, it is reasonable to believe that on both localities there is a shortage of suitable shells for *P. cuanensis* and *A. chiroacanthus*, and that the shell-less specimens live for a shorter time.

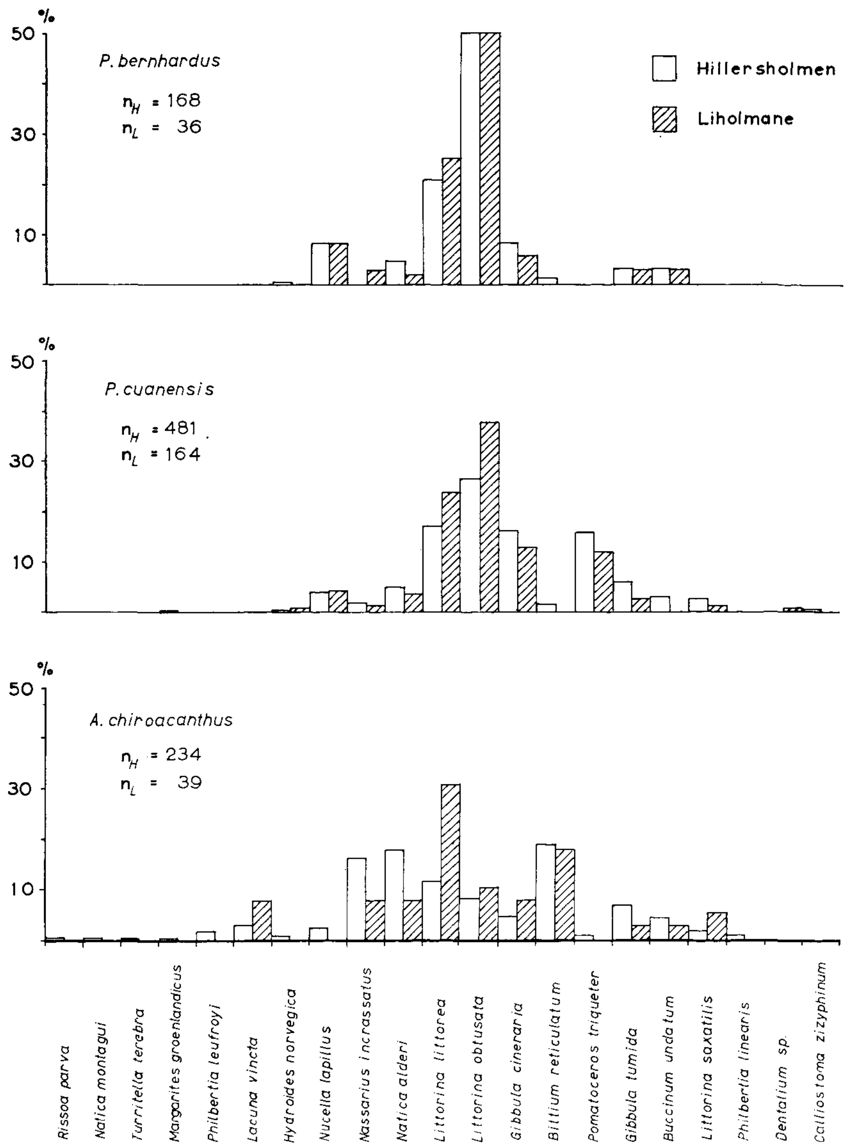

Fig. 16. Distribution of *Pagurus bernhardus*, *Pagurus cuanensis*, and *Anapagurus chiroacanthus* on types of shells. (n_H=No. of specimens from Hillersholmen, n_L=No. of specimens from Liholmane.)

The types of shells inhabited by *P. bernhardus*, *P. cuanensis*, and *A. chiroacanthus* are shown in Fig. 16. *P. bernhardus* was found in 10 species of shells of which *Littorina obtusata* (L.) and *L. littorea* (L.) constituted more than 70% of the shells on each locality. 15 types of shells were utilised by *P. cuanensis*, however, about 50% inhabited the two *Littorina* species. About 13% used fragments of *Pomatoceros*

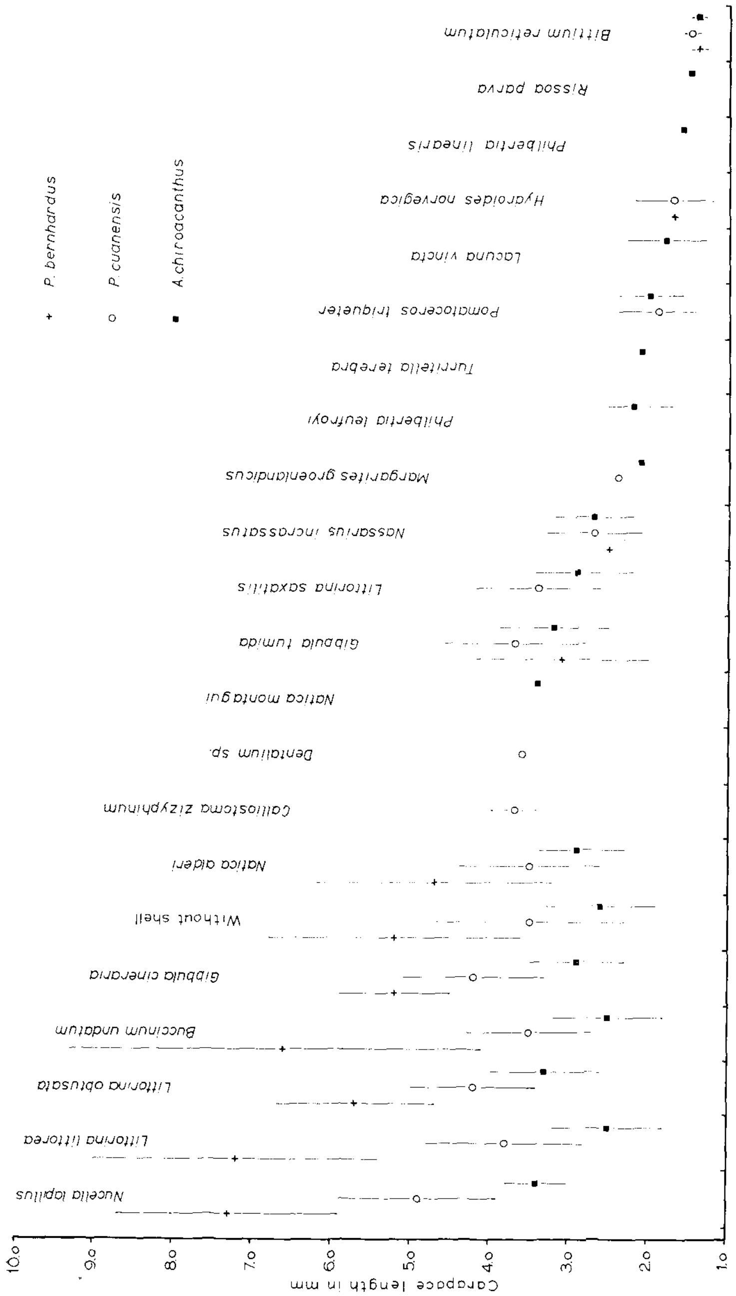

Fig. 17. Size distribution of *Pagurus bernhardus*, *Pagurus cuanensis*, and *Anapagurus chiroacanthus* and types of shells from Hillersholmen and Liholmane. Means and standard deviations have been calculated.

tubes as shell. Except for a few *A. chiroacanthus*, *P. cuanensis* was the only pagurid that utilised this kind of shell. *A. chiroacanthus* inhabited 19 species of shells, and *Bittium reticulatum* (DA COSTA) was especially used by this species. *P. prideauxi*, mainly collected at Hillersholmen, was found in the following shells: 14 *Littorina littorea*, 12 *Gibbula cineraria* (L.), 8 *Littorina obtusata*, 8 *Natica alderi* (FORBES), 5 *Buccinum undatum* L., 2 *Nucella lapillus* (L.), 1 *Calliostoma zizyphinum* (L.), 1 *Velutina velutina* (MÜLLER), and 1 in only *Adamsia palliata* which partly, or completely, covered all the shells. According to PIKE & WILLIAMSON (1959) *P. prideauxi* normally does not change its shell after attaining a carapace length of c. 8 mm as it is covered by the growing anemone.

Fig. 17 shows the size of *P. bernhardus*, *P. cuanensis*, and *A. chiroacanthus* inhabiting the different types of shells, and without shells. Their size always corresponded to the size of the shell they inhabited. The largest specimens were thus to be found in the shells of only the largest gastropod species while smaller specimens could be found in shells of appropriate size belonging to small species or young specimens of large species. Mainly larger *P. cuanensis* and *A. chiroacanthus* were found without shells. This may indicate that sufficient shells of e.g. *Pomatoceros* and *Bittium* are available for the small specimens, but that, as the pagurids grow, they will need larger shells which they may not find. Nevertheless they will still be forced to leave the small ones. This can be settled experimentally.

PARASITES

One species of epicaridean and five species of rhizocephalan parasites were found on five of the six species of Anomura (Table 4).

Three specimens of *G. intermedia*, all ♂♂, measuring 5.6 mm, 5.8 mm, and 5.9 mm were infected by the rhizocephalan, *Lernaeodiscus galatheae* SMITH, which also occurs on *Galathea dispersa* BATE (SMITH 1906). In the Scandinavian waters the parasite is only recorded from *G. intermedia* (BOSCHMA 1928).

Six specimens of *Peltogaster paguri* RATHKE were found on *P. bernhardus*. The hosts, 3 ♂♂ and 3 ♀♀, measured 5.0 mm, 5.5 mm, 6.2 mm and 5.8 mm, 5.8 mm, 7.2 mm. To make sure no confusion was made with *Clistosaccus paguri* LILLJEBORG, which has a superficial likeness with *P. paguri*, the specimens were sectioned for microscopical studies. 2.1% were infected, while DAHL (1949) had 16% from Nord-Tröndelag and northern Norway (museum collections). The reason for this high percentage is possibly that particularly infected specimens have been collected.

P. cuanensis was heavily infected as four species occurred on 10.4% of the animals. *Athelges paguri* RATHKE was found on 7 ♂♂ and 3 ♀♀ which together had an average length of 2.5 mm. According to PIKE (1961) two bopyrid species occur on *P. cuanensis*, viz. *Athelges bilobus* G. O. SARS with a northerly range, and *A. lorifera* HESSE with a southerly range. However, my specimens agreed more closely with the description of *A. paguri* by SARS (1899). 7 ♂♂ and 9 ♀♀ were infected by

Table 4. Epicaridean and rhizocephalan parasites from Hillersholmen (H) and Liholmane (L).

Host	Locality	Number of specimens examined	Number of specimens infected	Parasite
Galathea intermedia	H	1073	2	*Lernaeodiscus galatheae*
	L	347	1	*Lernaeodiscus galatheae*
Pisidia longicornis	H	938	0	None
	L	113	0	None
Pagurus bernhardus	H	238	6	*Peltogaster paguri*
	L	39	0	*Peltogaster paguri*
Pagurus cuanensis	H	577	8	*Athelges paguri*
	L	210	2	*Athelges paguri*
	H	577	13	*Peltogaster paguri*
	L	210	3	*Peltogaster paguri*
	H	577	32	*Peltogaster curvatus*
	L	210	11	*Peltogaster curvatus*
	H	577	11	*Gemmosaccus sulcatus*
	L	210	2	*Gemmosaccus sulcatus*
Pagurus prideauxi	H	51	1	*Athelges* sp.
	L	1	0	*Athelges* sp.
Anapagurus chiroacanthus	H	336	3	*Peltogaster paguri*
	L	73	0	*Peltogaster paguri*
	H	336	2	*Gemmosaccus sulcatus*
	L	73	0	*Gemmosaccus sulcatus*

Peltogaster paguri, one on each host. The mean length of the hosts was 4.3 mm. *Peltogaster curvatus* KOSSMANN occurred on 43 specimens (SAMUELSEN 1970). The fourth parasitic species on *P. cuanensis* was *Gemmosaccus sulcatus* (LILLJEBORG). The parasite was found on 7 ♂♂ and 6 ♀♀. The mean length of the hosts was 4.7 mm. Each host carried from 1 to 7 *G. sulcatus*, with a mean of 3.

One *P. prideauxi*, a ♀ measuring 9.9 mm, was infected by *Athelges* sp. The species fits the description of *A. prideuaxi* GIARD and BONNIER (redescribed by PIKE 1953) concerning the ♂ and the terminal segment of the metasome of the ♀. However, the first oostegite, somewhat damaged, was more like that of *A. paguri* RATHKE. To make a correct identification additional *Athelges* have to be collected from *P. prideauxi*.

Peltogaster paguri occurred on *A. chiroacanthus* too. 2 ♀♀, which measured 2.1 mm and 2.5 mm, and a ♂, 3.6 mm long, were infected by one parasite each. 2 ♀♀ with lengths of 3.2 mm and 3.5 mm, were hosts for 2 and 4 specimens of *Gemmosaccus sulcatus* respectively.

None of the infected ♀♀ of any of these species carried eggs, although in many cases they were collected during the breeding period.

PREDATORS

To find possible predators of the anomurans, fishing nets were placed across the sound at Hillersholmen (28 to 29 June 1968). The following species were caught and examined for stomach contents: 6 *Gadus morrhua* L., 4 *Pollachius pollachius* (L.), 3 *Labrus ossifagus* L., 13 *Labrus berggylta* ASCANIUS, 1 *Centrolabrus exoletus* (L.), 2 *Callionymus lyra* L., and 9 *Microstomus kitt* (WALBAUM).

Labrus berggylta appeared to be the most important predator as 8 *P. bernhardus*, 5 *P. cuanensis*, 8 *A. chiroacanthus* and parts of a pagurid, inside a broken *Natica alderi*, were identified. In addition 1 *Galathea squamifera* was found. In *Labrus ossifagus* I found 1 *G. intermedia*, while parts of *Galathea strigosa* and brachyurans occurred in the stomachs of *Gadus morrhua*. *P. longicornis* and *P. prideauxi* were not found in either of the fishes. The porcellanid crab may be protected by its hiding habit (see p. 37), and the pagurid by the sea anemone, *Adamsia palliata*, as suggested by PIKE (1961).

Of other possible predators in the area only a few specimens of *Cancer pagurus* L. and *Homarus gammarus* (L.) have been observed. It seems therefore likely that the main predators are the labrids which according to QUIGNARD (1966), and my own observations, are common in shallow water only during the summer.

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