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The distribution and habitats in the North Atlantic of two gnathiid species (Crustacea, Isopoda) and their reproductive biology in the Denmark Strait and north of Iceland

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Contribution from the BIOICE programme
(Benthic Invertebrates in Icelandic Waters)

Anne B. Klitgaard

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Contents

The distribution and habitats in the North Atlantic of two gnathiid species (Crustacea, Isopoda) and their reproductive biology in the Denmark Strait and north of Iceland

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Caecognathia robusta and *C. abyssorum* (Crustacea, Isopoda, Gnathiidae) were found associated with several species of demosponges collected in the Denmark Strait and around Iceland. Comparison of the distribution of the two gnathiid species shows *C. robusta* to be mainly a cold water species occurring north of the Greenland-Iceland-Faroe Ridge, while *C. abyssorum* is principally an Atlantic species occurring south of this ridge system; the distribution of the two species, however, overlaps in the Denmark Strait. Both gnathiid species demonstrate a well-developed adaptability to utilize the naturally occurring cavities. *C. robusta* inhabits such different cavities as the massive, well-defined preoscular cavities of the spherical *Geodia mesotriaena* and the lacunae of the soft, elastic, encrusting *Hexadella dedritifera*. *C. abyssorum* shelters in the lacunae in the encrusting *H. dedritifera*. The female: male ratio for both gnathiid species seems to be determined by the volume of the chosen cavity. Both species are primarily monogamous and each adult male, instead of having a "harem", appears to survive long enough to complete two or more consecutive female reproductive sequences. There is indication of continuous reproduction in *C. robusta* and perhaps also in *C. abyssorum*. The females of the two gnathiid species produce bigger and, in *C. abyssorum*, fewer pranizae than reported for "harem" forming gnathiid species.

Keywords: Gnathiidae, Isopoda, Northern Atlantic, distribution, monogamy, reproduction, sponge associations, habitats, biology.

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Introduction

Detailed descriptions of the morphology of the isopod family Gnathiidae have been given by Monod (1926) and Cals (1972). In Monod (1926) was also presented a classification of the 62 species then known. In the most recent revision of the family (Cohen & Poore 1994) a new classification is proposed on the basis of the 155 species recognized today. Cohen & Poore revived the genus *Caecognathia*, previously synonymized with *Gnathia* and transferred several species from *Gnathia* to *Caecognathia* including the two species *C. robusta* (G. O. Sars, 1879) and *C. abyssorum* (G. O. Sars, 1872) treated in the present paper.

Knowledge of biology and life cycles of Gnathiidae is only slowly emerging. Mouchet (1928) described the life cycle of *Gnathia maxillaris* (Montagu, 1804), and showed that three praniza stages precede the final transition to the adult state. Subsequently three praniza stages were discovered in the intertidal *Paragnathia formica* (Hesse, 1864) (Stoll 1962). Detailed descriptions of life history and developmental stages have been published for *P. formica* (Upton 1987a, b), *Caecognathia calva* (Vanhöffen, 1914) (Wägele 1987, 1988) and *C. abyssorum* (Klitgaard 1991).

Gnathiid juveniles, the pranizae, have a cone of piercing-sucking mouthparts and are generally regarded as being ectoparasites of fish, sucking the blood of the fish. The three praniza stages are active stages, where the pranizae swim in search of a fish host. Pranizae, newly released from the maternal marsupium, and recently moulted pranizae of the two consecutive developmental stages have an empty gut and a segmented pereon. After having had a meal of fish blood, the gut is filled and the elastic cuticle of the central pereonites is extended, causing the pranizae to stretch and the pereonal segmentation to be partially lost. The satiated pranizae detach from the fish host and shelter in suitable cavities as for example in sponges where a resting and digesting phase is followed by a moult into either the next stage of larger segmented praniza or into an adult male or female (Wägele 1987, 1988; Klitgaard 1991). Morphological investigations of the pranizae have been carried out, particularly of the structures involved in blood feeding, that is of the mouthparts (Cals 1978; Davies 1981; Charmantier & Euzet 1987) and of the digestive tract (Juilfs & Wägele 1987). The fish host of the pranizae has, however, only infrequently been identified (Monod 1926; Davies 1982; Wägele 1988; Rokicki et al. 1992; Arthur & Albert 1994).

The "harem" phenomenon in Gnathiidae, that is one male living together with several breeding females, was first described by Monod (1926) for *Paragnathia formica*, and later on confirmed in the same species by Upton (1987a, b). Likewise *Caecognathia calva* was found living in large "harems" in small hexactinellid sponges in the Antarctic (Wägele 1988).

The formation of "harems" has also been suggested for *C. abyssorum* by Klitgaard (1991) and *C. robusta* by Barthel & Brandt (1995). New data regarding the biology of both species have been obtained during the examination of a large number of demosponges collected in the Denmark Strait and around Iceland. These data show an other mode of living arrangement, both species primarily living in monogamous relationships, that is one male together with one female.

Both gnathiids have previously been reported associated with sponges; *Caecognathia robusta* with "a calcareous sponge" (Hansen 1916) and *Geodia mesotriaena* (Hentschel, 1929) and *Sycon* sp. (Calcarea) (Barthel & Brandt 1995) and *C. abyssorum* with *Halichondria tenuiderma* Lundbeck, 1902, "a sponge" (Hansen 1916; Monod 1926) and *Stryphnus ponderosus* (Bowerbank, 1866), *Stelletta normani* Sollas, 1880, *Tragosia infundibuliformis* (Fleming, 1866), *Axinella arctica* (Vosmaer, 1885) and *Phakellia robusta* Bowerbank, 1866 (all Demospongiae) (Klitgaard 1991).

In the present investigation *C. robusta* was found associated with four species of demosponges: *Geodia mesotriaena*, *Thenea valdiviae* Lendenfeld, 1906, *Hexadella dedritifera* Topsent, 1913 and *Pseudosuberites hyalinus* (Ridley & Dendy, 1887) and *C. abyssorum* with one demosponge, *H. dedritifera*.

Material and methods

Field sampling and laboratory procedure

Sponges were collected around Iceland during BIOICE (Benthic Invertebrates in Icelandic Waters) cruises in 1991, '92, '93, '94 and during a cruise with R/V *Paamiut* in the Denmark Strait (Greenland Institute for Natural Resources) in 1994.

The standard sampling gear used on the BIOICE cruises were detritus sledge, Rothlisberg & Pearcy epibenthic sledge, triangular dredge and Agassiz trawl. All sampling on R/V *Paamiut* were done with bottom trawl (mesh diameter 20 mm).

All sponges were sorted as soon as the sample came onboard. On BIOICE cruises a representative selection of the different species on each station was kept. On R/V *Paamiut* the number of *Geodia mesotriaena* was very large on one station (GF 94PA0090002, Table 2) and in this case the maximum dimension of all specimens was measured on board and only a selection of whole specimens was preserved while the preoscular cavities of the majority of the specimens were cut out and kept. All specimens of this species were kept on the remaining stations. A representative selection of other sponge species was kept on all stations.

The sponges were fixed in 4% borax-buffered formaldehyde and after at least two to three weeks rinsed in freshwater and transferred to 80% ethanol.

Before examining the sponges for associated fauna, the maximum dimensions of each specimen of *Geodia mesotriaena* and of the four species of *Thenea* were measured (Table 1). The number of excurrent openings of each specimen of *G. mesotriaena* was counted and the maximum diameter of each opening measured to nearest 0.01 cm.

Examination of the sponges for associated gnathiids included cutting open the preoscular cavities of all specimens of *G. mesotriaena*, examining the in- and excurrent furrows, osculae and spicule "fur" of the four *Thenea* species and carefully picking in pieces specimens of *Hexadella dedritifera* as well as a fragment of *Pseudosuberites hyalinus* under a stereomicroscope.

Some other *Geodia mesotriaena* material was also examined: Collections made on survey cruises by the Greenland Institute for Natural Resources, the Danish Ingolf Expedition (1895-96), the Lynch Expedition (1972) and R/V *Polarstern* cruise ARK VII/2 (1990) at NE-Greenland. All sponge material is kept at the Zoological Museum, University of Copenhagen and the Icelandic Institute of Natural History, Reykjavik.

The number of gnathiids of each sponge specimen was counted and the location of the gnathiids in the sponge was registered. Identifications of the gnathiids were made following the descriptions of Sars (1885, 1899), Hansen (1916) and Monod (1926). Adult males of *Caecognathia robusta* were compared with the type material of *Anceus robustus* G. O. Sars, 1879 (Catalog No. F1728, Zoological Museum, Oslo), and with adult males sampled at two stations of the Danish Ingolf Expedition (1895-96) and at two stations of the Ryder Expedition (1891-92) identified by H. J. Hansen (1916) (CRU 1569-1572 Zoological Museum, Copenhagen) as well as with specimens collected at NE Greenland in 1994 in association with *Geodia mesotriaena* (Barthel & Brandt 1995). Adult males of *C. abyssorum* were compared with specimens collected at the Faroe Islands (Klitgaard 1991). The present material of *Caecognathia robusta* and *C. abyssorum* is kept at the Icelandic Institute of Natural History, Reykjavik and the Zoological Museum, Copenhagen.

The total length of the gnathiids was measured from the front margin of the head (adults) or from the apex of the mouthparts (pranizae) to the apex of the pleotelson to closest 0.1 mm. In addition the maximum width of the head of the males of *C. robusta* was measured to closest 0.01 mm.

Females containing embryos were dissected and the number and total length of the embryos registered.

As an attempt to identify the pranizae the number of flagellar articles of antenna 2 were counted in a number of these as well as in a number of adults of *C. robusta* and *C. abyssorum*. For comparison the number of flagellar articles of antenna 2 were also counted in some adults and pranizae of *C. abyssorum* collected at the Faroe Islands (Klitgaard 1991).

Subjective estimates of the digestive caeca of the adult males of both species were recorded as index scores on a discrete trinary scale as follows: I: two large digestive caeca, occupying most of pereon; II: two reduced digestive caeca, occupying half or less of pereon; III: no visible digestive caeca, pereon appearing hollow.

Distribution maps of *C. robusta* and *C. abyssorum* were prepared using the Geographic Information System MapInfo for Windows 3.0 (licens no. 30200123) and the American Digital Cartography's (ADC) WorldMap for MapInfo digital atlas (ed. 1, June 1993).

Results

Geographical distribution of *Caecognathia robusta* and *C. abyssorum*

Caecognathia robusta has previously been recorded fourteen times in different parts of the Northeast Atlantic (including the Norwegian Sea, the Greenland Sea, the Barents Sea and the Arctic Sea) at depths between 314 and 884 m as well as at one station in Baffin Bay at 208 m. In addition it has previously indirectly been reported from one station north of Svalbard at 1000 m (see "The habitats of gnathiids") (Fig. 1, Table 2).

The new records of *C. robusta* agree with the previously known distribution (Fig. 1, Table 3). The finds of *C. robusta* at R/V *Ingolf* St.no. 90 west of Iceland at 1070 m, R/V *Polarstern* St.no. 223 in the Fram Strait and BIOFAR St.no. 041 southeast of the Faroe Islands constitute respectively the hitherto deepest, most northerly and most southerly records of the species. The known temperature range of the species is from –0.60 to +5.80 °C (Tables 2 and 3).

Caecognathia abyssorum has previously been recorded from 32 stations in the NE-Atlantic (including the Norwegian Sea and the Greenland Sea) in depths between 130 and 913 m (Fig. 2, Table 2). The species was in the present

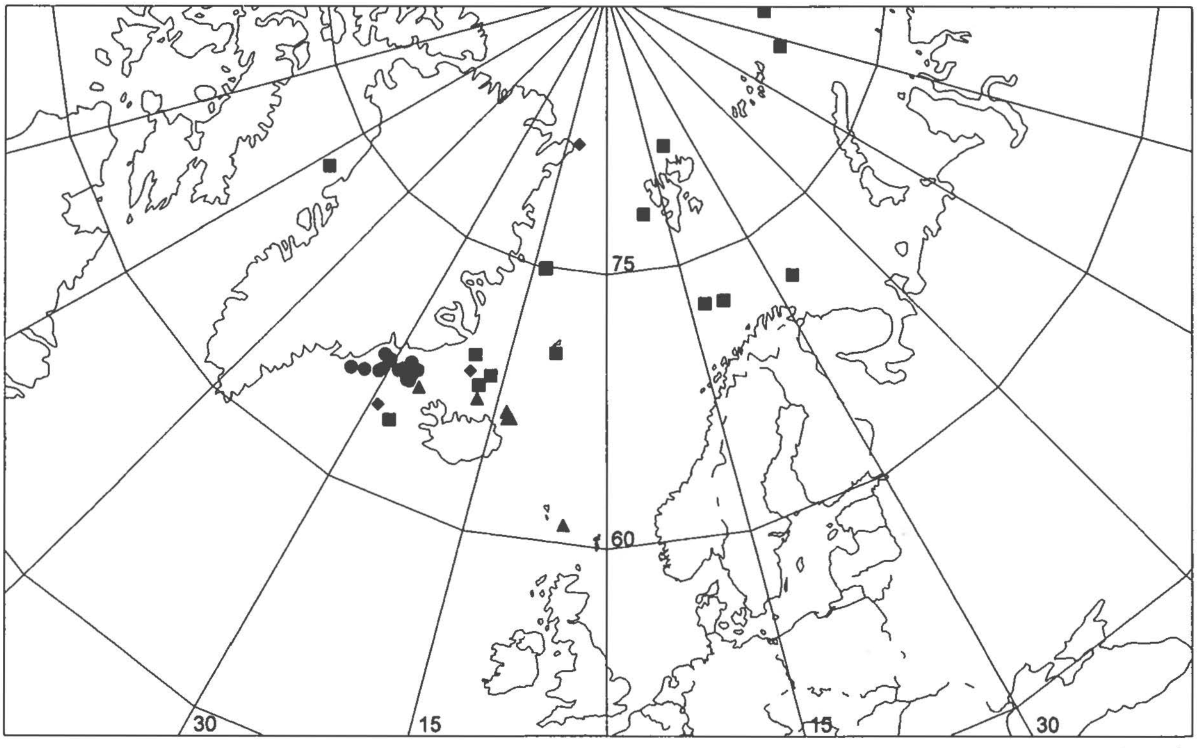


Fig. 1. Distribution of *Caecognathia robusta*. ■ = previous records, ● = GF stations, ▲ = present BIOICE and BIOFAR stations, ◆ = Ingolf Exp. St.no. 90, Lynch Exp. St.no. 9, R/V *Polarstern* St.no. 223.

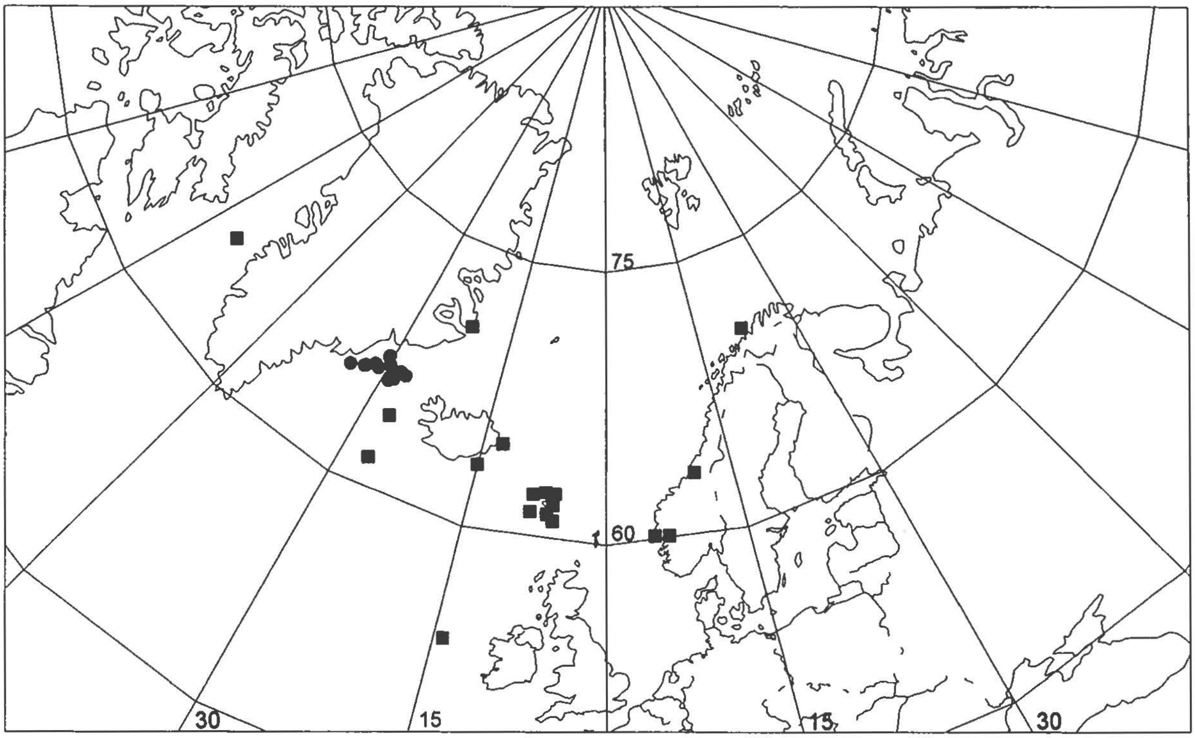


Fig. 2. Distribution of *Caecognathia abyssorum*. ■ = previous records, ● = GF stations. The BIOFAR stations at the Faroe Islands reported in Klitgaard (1991) are situated very close to each other, and only a representative number of these are indicated.

investigation found at thirteen stations in the Denmark Strait at depths between 282 and 467 m (Fig. 2, Table 3). The temperature range for *C. abyssorum* is here reported as 0.04-9.80 °C (previously 4.0-9.8 °C) (Tables 2 and 3).

The sponges

Seven sponge species were examined, all Demospongiae, and representing three orders (Hartman 1982) (Table 1). *Geodia mesotriaena* has a dominant mineral skeleton of silica spicules giving the sponge a very solid texture, and a cortex of globular microscleres (sterrasters). It is very regular in body shape being spherical to slightly flattened. Most frequently a specimen has one apical excurrent opening. Often several osculae are concentrated in a preoscular cavity under the top excurrent opening. Occasionally two or more excurrent openings are present distributed on the upper side of a specimen.

According to Steenstrup & Tendal (1982) four species of the genus *Thenea* are recognized in the North Atlantic, all having a thick "fur" of vertically oriented spicules on the surface. *Thenea valdiviae* is sphere-shaped or lump-

Plate I.

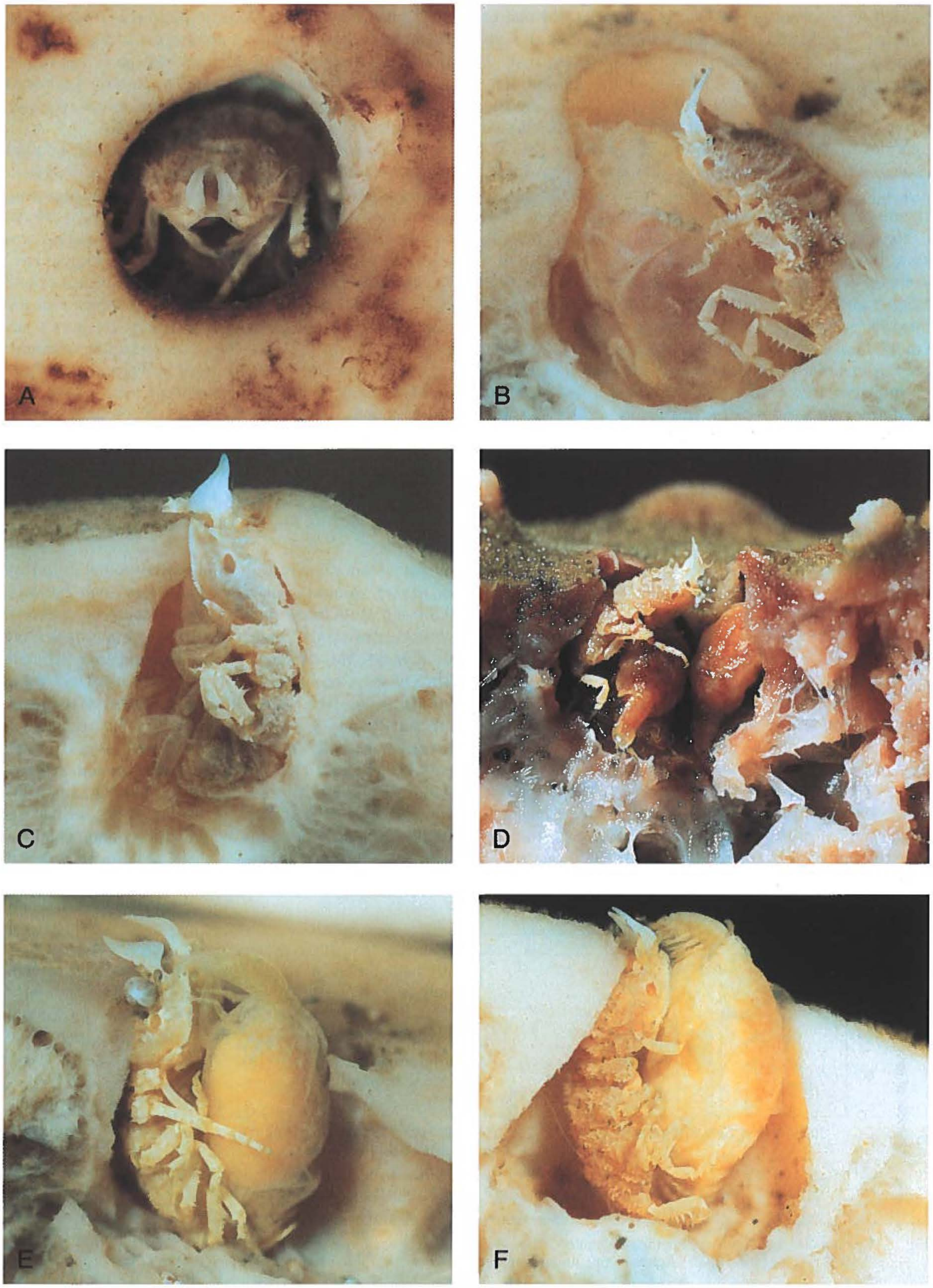
A. Male of *Caecognathia robusta* sitting in a preoscular cavity in *Geodia mesotriaena* with the mandibles protruding from the excurrent opening (St.no. GF 94PA0090002).

B. Part of the wall of a preoscular cavity in *Geodia mesotriaena* has been removed to show a pair of *Caecognathia robusta*. The male is sitting dorsally on the mature female having the mandibles in the excurrent opening (St.no. GF 94PA0090002).

C. Male of *Caecognathia robusta* in a preoscular cavity of *Geodia mesotriaena* of restricted volume (St.no. GF 94PA0090002).

D. Male of *Caecognathia robusta* together with three females, one mature female (at the bottom, only the head is visible) and two swollen pranizae of third stage respectively, within a preoscular cavity in *Geodia mesotriaena*. The male is positioned on top of the females with the head in the excurrent opening (St.no. BIOICE 2022).

E, F. Two cases of a male of *Caecognathia robusta* sitting in a preoscular cavity in *Geodia mesotriaena* holding on to a praniza with the pereopods. The praniza in both E and F has the pleon in the excurrent opening and the head in the preoscular cavity (St.no. GF 94PA0090002).


A
B
C
D
E
F

formed with an equatorial incurrent furrow, and one or more osculae distributed on top of the body. *T. levis* Lendenfeld, 1906 is elongate, sometimes crescent-shaped, with long in- and excurrent furrows on the opposite long sides. *T. abyssorum* Koltun, 1959 is triangular to mushroom-shaped, always with only one osculum positioned opposite of the incurrent furrow. *T. muricata* (Bowerbank, 1858) is mushroom-shaped to ovate or hemispherical with one or more osculae distributed on the domed summit.

Hexadella dedritifera is an encrusting species growing as a thin carpet on the sediment surface substituting a skeleton by incorporating foreign bodies (Topsent 1913; Hentschel 1929). Fragments of bryozoans, foraminiferans, foreign sponge spicules, sand grains and very small, young specimens of geodiids were observed within the present material of this species. It was also found as an episponge on the geodiid *Isops phlegraei* Sollas, 1880, most frequently present on the incurrent surface of *I. phlegraei* using the spicule "fur" as a substitute for a skeleton. The two different habitats of *H. dedritifera* are in the text referred to as "free living" and "episponge" respectively.

Pseudosuberites hyalinus is a somewhat lumpy sponge with an elastic consistency. Only a minor fragment of this species was however examined in the present investigation.

Occurrence of the gnathiids in *Geodia mesotriaena*

See Table 4. The data indicate a more frequent association of *C. robusta* with *G. mesotriaena* north of Iceland; however, only a small number of sponge specimens have been sampled in that area and further material is necessary to confirm this apparent tendency. Only one specimen collected during the Ingolf Expedition was inhabited; it must, however, be kept in mind that the previous treatment of these sponges is not known. It is not possible to deduce anything about the frequency of *C. robusta* in the collections of respectively the Lynch Expedition and the R/V *Polarstern* cruise ARK VII/2 as only a very limited number of sponges have been sampled.

All individuals of *Caecognathia robusta* were found inside the preoscular cavities of *Geodia mesotriaena*; in four sponges a male was found in an osculum opening into a preoscular cavity. There was, however, always only one adult male per cavity; when a male was present in an osculum, no male was found in the preoscular cavity and vice versa. The males were usually positioned either with the head in the excurrent opening with the mandibles protruding from the opening, or entirely inside the opening (Pl.I, A). When present in an osculum, those males similarly had the head in the opening of the osculum. Some males were holding on to a praniza with the pereopods, the praniza having the pleon in the excurrent opening and the head in the preoscular cavity, apparently so positioned at the time of capture (Pl. I, E, F). When a mature female was present in the cavity, the male was most often found sitting dorsally on the female having the head in or right inside the excurrent opening (Pl. I, B).

Fig. 3 shows that most gnathiids were found in sponges having excurrent openings with diameters between 0.30 and 0.49 cm. A total of 841 excurrent openings were measured. Of these 108 (12.8%) were occupied by *C. robusta*. However, 215 excurrent openings (25.6%) were in the size category 0.30-0.49 cm and 81 of these openings (37.7%) were inhabited by this gnathiid, in contrast to only 4.3% of the rest of the excurrent openings. If only the occupied excurrent openings are considered, then 75% of these had a diameter between 0.30 and 0.49 cm, while 9.3% had a diameter smaller than 0.30 cm and 15.7% a diameter bigger than 0.49 cm. A positive correlation was found between the diameter of inhabited excurrent openings and the maximum width of the head of the males of *C. robusta* (Spearmans correla-

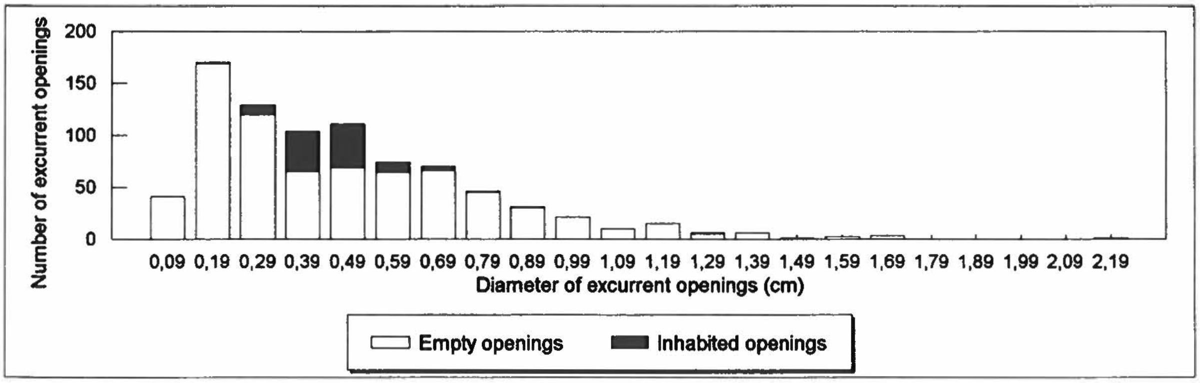


Fig. 3. Frequencies of excurrent opening diameters in *Geodia mesotriaena*. Diameter intervals are 0.00-0.09, 0.10-0.19, 0.20-0.29,.....2.10-2.19 cm. Number of excurrent openings occupied by *Caecognathia robusta* is indicated ("inhabited openings") for each interval.

tion coefficient, rs = 0.392; $p < 0.001$; α = 0.05). In the four cases where a male was found in an osculum, the diameter of the osculae was between 0.25 and 0.39 cm while the diameter of the excurrent openings was between 0.74 and 1.33 cm. Thus, the gnathiids occasionally inhabit preoscular cavities with large excurrent openings if osculae with suitable diameters are present in the cavities.

A local variation in the occurrence of *C. robusta* is demonstrated between the two GF stations in the Denmark Strait where most specimens of *G. mesotriaena* were sampled (St.no. GF 94PA0090001, 131 specimens and GF 94PA0090002, 316 specimens, Table 3), on which the gnathiid was present in respectively 8.4 and 25.3% of the specimens. Comparing the diameters of the excurrent openings of the specimens from the two stations shows that 18.6% of all measured openings from St.no. GF 94PA0090001 had a diameter between 0.30 and 0.49 cm while 30.1% of the excurrent openings from St.no. GF 94PA0090002 were in this interval. Thus, differences in the occurrence of excurrent openings of a suitable diameter might constitute an explanation to observed local differences in the occurrence of gnathiids in *G. mesotriaena*.

The distribution of males and females of *C. robusta* in the preoscular cavities is shown in Table 5. Most inhabited cavities were occupied by either 1 ♂ or 1 ♂ + 1 ♀ (praniza or mature female). Only 9.9% of the inhabited cavities contained 1 ♂ + 2 ♀ or 1 ♂ + 3 ♀. Four of the seven single females were ovigerous, one contained embryos and in two cases the female was empty and crumpled. In seven cavities a single praniza was present, two of these with eggs just visible in twin ovaries, lying mid-dorsally in the pereon (as described in Upton 1987a). In two cavities the dead remains (a "skull") of a male were found. In each case the sponge had begun to grow up around the remains embedding them in the tissue. In addition in one cavity occupied by one adult male and one female, a "skull" of a dead male was found in a small cavity right under the preoscular cavity.

If only considering the preoscular cavities occupied by a male together with one or more females (58 cavities, Table 5) it appears that 46 (79.3%) of these cavities contained 1 ♂ + 1 ♀, 9 cavities (15.5%) contained 1 ♂ + 2 ♀ and 3 cavities (5.2%) contained 1 ♂ + 3 ♀. Four of the 8 BIOICE preoscular cavities were occupied by 1 ♂ + 1 ♀, 2 cavities contained 1 ♂ + 2 ♀ and 2 cavities contained 1 ♂ + 3 ♀. All BIOICE sponges containing a male with more than one female were collected north of Iceland. In comparison the GF samples yield 47 preoscular cavities containing a male together with female(s) with respectively 40 cavities (85.1%) 1 ♂ + 1 ♀, 6 (12.8%) 1 ♂ + 2 ♀ and 1 (2.1%) 1 ♂ + 3 ♀. However, when a chi-square test with Yates' correction is applied to the above data, no significant difference is found (chi-square = 3.30 with 1 d.f.; $0.05 < p < 0.10$).

Occurrence of the gnathiids in *Hexadella dedritifera*

Caecognathia robusta and *C. abyssorum* were both found in *Hexadella dedritifera*. In Tables 6 and 7 are shown the number of individuals of the two species as well as of pranizae found singly respectively in the free living specimens and in the episponge specimens on *Isops phlegraei*. In addition the number of specimens of *I. phlegraei* on which gnathiids were found are given (Table 7). All gnathiids were found inside small cavities in *H. dedritifera*, these cavities probably constituting a part of the water canal system (O. S. Tendal pers. comm.). *Caecognathia robusta* and *C. abyssorum* were both present exclusively as either single males or pairs (one male together with one female; praniza or mature female). In a few cases single females were found. However, these were either ovigerous (one *C. robusta*, Table 6 and two *C. abyssorum*, Table 7) or contained embryos (one *C. abyssorum*) or were empty and crumpled (one *C. abyssorum*). In addition dead remains of males of both gnathiid species were found in a number of cavities. Two adult males of *Caecognathia hirsuta* (G. O. Sars, 1877) were found in *H. dedritifera* in a free living specimen (Table 6) and in an episponge specimen on *I. phlegraei* (Table 7) respectively. A large number of pranizae (segmented as well as swollen pranizae) of varying sizes (1.7-6.2 mm) were present in particularly the free living specimens of *H. dedritifera* (Table 6). The pranizae were found singly, the majority squeezed into small cavities.

A comparison between the total numbers of *C. robusta* and *C. abyssorum* (Tables 6 and 7) shows that the two species are almost equally well represented in the free living specimens of *H. dedritifera*, *C. robusta* being only slightly more frequent than *C. abyssorum*. *Caecognathia abyssorum* is dominant in *H. dedritifera* growing as episponge on *I. phlegraei*; only two adult males of *C. robusta* were found in the latter case. In addition the data in Table 6 show a tendency towards one of the two gnathiid species being more frequent than the other on each separate station in the free living specimens of *H. dedritifera*. On two stations only pranizae were found.

The general impression, when examining the material of *H. dedritifera*, was that the gnathiids displayed a clumped distribution. *C. abyssorum* was observed to concentrate in small patches, like small "villages", in *H. dedritifera*; thus pairs as well as single males were often found in separate cavities situated in close proximity to each other, sometimes with only few millimeters between. For example, *C. abyssorum* and single pranizae were found in *H. dedritifera* on eleven specimens of *I. phlegraei* on St.no. GF 94PA0090026 (Table 7), but the majority of the gnathiids (73.5%) were present on three of the specimens. The same applies to *C. robusta* in the specimens of free living *H. dedritifera* (Table 6).

Occurrence of the gnathiids in the four species of *Thenea* and in *Pseudosuberites hyalinus*

Even though a large number of specimens of all four species of *Thenea* were examined (Table 1), gnathiids were found exclusively in *T. valdiviae*, the only exception being one swollen praniza of unknown identity present on a *T. muricata*. Gnathiids were, however, only present in eight of the 389 (2.1%) examined specimens of *T. valdiviae* (Table 8). *Caecognathia robusta* was found inside the osculum of four specimens; in two of these one adult male was sitting dorsally on a mature female with the head in the opening of the osculum and in the other two a single adult male was present. The two single males both had a soft, transparent cuticle and might therefore recently moulted to the adult stage. A swollen praniza was found in the incurrent furrow of two sponge specimens (BIOICE 2010 and BIOICE 2033) and in the fringe of spicules on the upper rim of the incurrent furrow of one specimen (BIOICE 2089). Three segmented pranizae were found in the spicule "fur" of two specimens (Table 8). The pranizae were of varying body size (2.6-5.9 mm) and of unknown identity.

One adult male of *Caecognathia robusta* was found inside a small cavity in a fragment of *Pseudosuberites hyalinus* together with the remains of a dead male (Table 8).

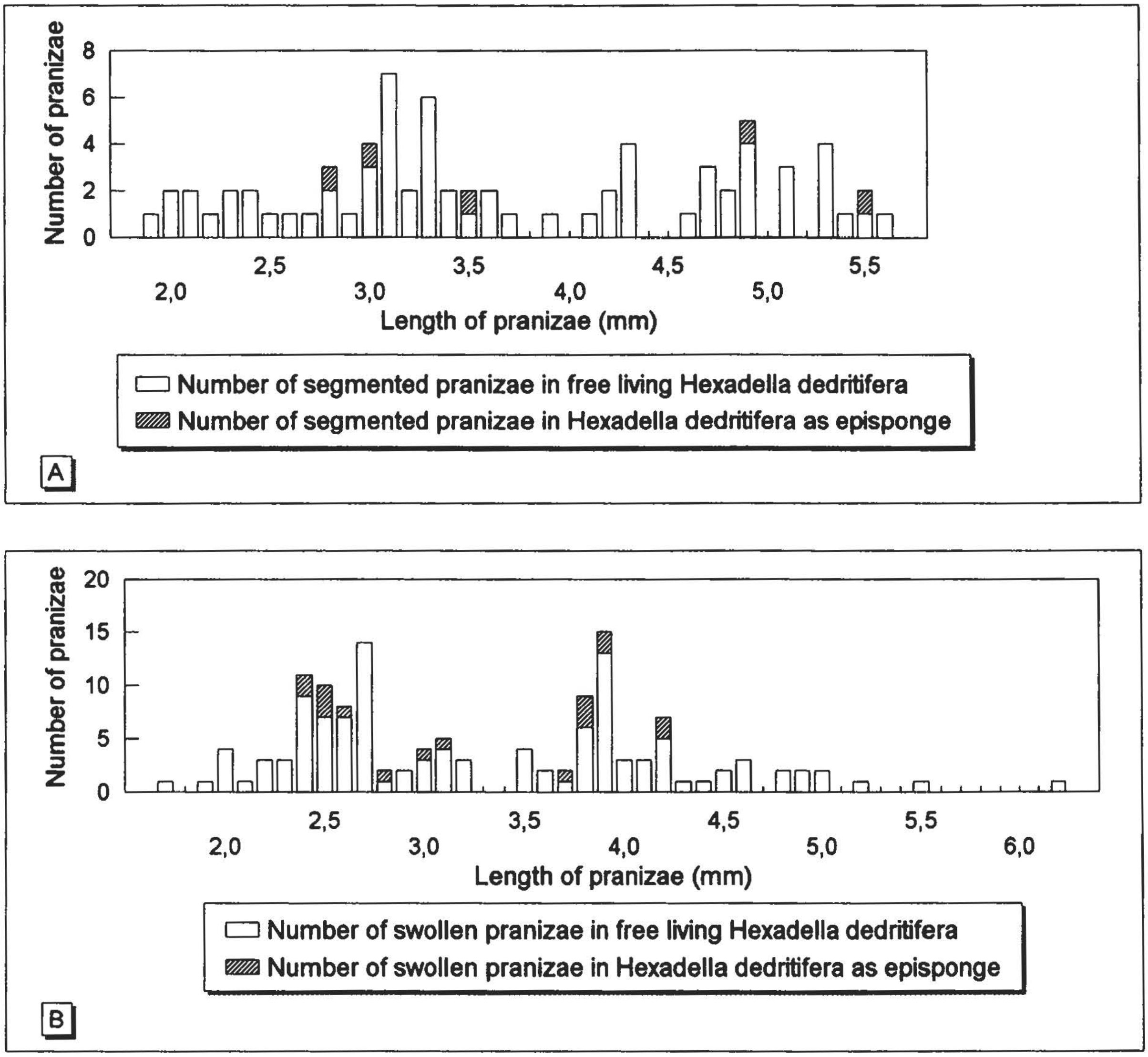


Fig. 4. Length frequencies of pranizae (A: segmented pranizae, B: swollen pranizae) found singly in *Hexadella dedritifera* respectively in free living specimens and in episponge specimens on *Isops phlegraei*. Only intact pranizae were measured (116 swollen pranizae/68 segmented pranizae in the free living specimens and 17 swollen pranizae/5 segmented pranizae in episponge specimens on *I. phlegraei*).

Length measurements of adults and pranizae

In Tables 9 and 10 the results of the length measurements of adult males and females of *Caecognathia robusta* and *C. abyssorum* are summarized. In addition the length of the swollen pranizae found together with adult males of the two species are shown. The total length of both adult males and females of *C. robusta* is very variable, the length of the males varying from 4.1 to 8.1 mm and of the females from 4.3 to 7.1 mm (Table 9). A significant difference between the means was found, the females being smaller than the males (t-test, $t = 3.11$ with 181 d.f.; $p < 0.01$). In addition a comparison of the males of *C. robusta* inhabiting respectively *Geodia mesotriaena* (GF samples) and *Hexadella dedritifera* (GF samples) (Table 9), also showed a significant difference between the means, the males in *G. mesotriaena* being larger than the males in *H. dedritifera* (t-test, $t = 7.52$ with 105 d.f.; $p < 0.01$).

A variation in the total length of adult males and females of *C. abyssorum* is also seen in the GF material (Table 10), this variation being, however, not as pronounced as in *C. robusta*. A marked difference in average length is seen, when the material from the Denmark Strait (GF samples) is compared with sponge associated individuals from the Faroe Islands (Klitgaard 1991). The Greenlandic specimens being 1.3 mm (both ♂ and ♀) longer in average than the Faroese specimens, and the maximum length of both males and females from the Faroe Islands is smaller than the minimum length of the GF specimens. A significant difference between the means of males and females of *C. abyssorum* was found, the females being larger than the males in both the GF samples (t-test, $t = 3.04$ with 89 d.f.; $p < 0.01$) and the BIOFAR samples (t-test, $t = 3.00$ with 39 d.f.; $p < 0.01$).

The majority of the pranizae (152) present singly in *H. dedritifera* were swollen with a full gut and a dilated pereon. A number of segmented pranizae (77), with a completely segmented pereon, the "pullus" stage of Monod (1926), were, however, also found in this sponge species. The length frequencies of both types of pranizae are shown in Fig. 4. As can be seen the length frequencies of swollen pranizae as well as of segmented pranizae in *H. dedritifera* growing as episponge on *Isops phlegraei* supplement very well the frequencies of both praniza types in the free living specimens of this sponge species. One peak is seen for the segmented pranizae about 3.1-3.3 mm and a somewhat more diffuse peak about 4.9 mm (Fig. 4A). Similarly, two peaks can be discerned for the swollen pranizae; one about 2.4-2.7 mm and one about 3.9 mm (Fig. 4B).

Number of flagellar articles of antenna 2

Monod (1926) mentioned that the pranizae of *Caecognathia abyssorum* have six flagellar articles on antenna 2, as do the adults of this species. This differs from the seven flagellar articles of antenna 2 of adults of *C. robusta*; the number of flagellar articles is unknown for the pranizae of this species. To examine whether this character can be used to discern between the pranizae of these two gnathiid species and if so to identify the pranizae found singly in *Hexadella dedritifera* the number of flagellar articles of antenna 2 were counted for a number of the present pranizae and adults of *C. robusta* and *C. abyssorum* as well as of single pranizae found in *Hexadella dedritifera* (Table 11).

Number of embryos in females

A total of eight adult females of *C. robusta* and seven of *C. abyssorum* contained embryos (Table 12). The number of embryos per female ranges from 59 to 175 in *C. robusta* and from 16 to 58 in *C. abyssorum*, and is increasing with female size in *C. robusta* (Spearmans correlation coefficient, $rs = 0.986$; $p < 0.01$; $\alpha = 0.05$), while no significant relationship was found for *C. abyssorum* (Spearmans correlation coefficient). The average number of embryos per brood is very different in the two species, *C. robusta* producing an average of 110±42.7 while this number is 33±16.5 for *C. abyssorum*.

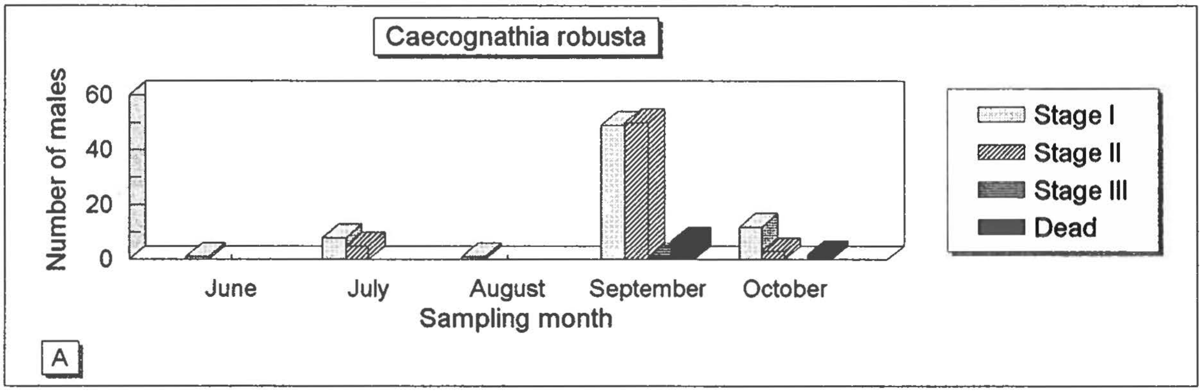
The average length of the embryos, representing different developmental stages, of both species varies, as can be seen from Table 12. One of the females of *C. robusta* contained very young embryos (marked with a "+" in Table 12). These had no eyes or mouthparts and were very adherent and fragile, which made them impossible to count or to measure their total length.

A tendency was seen regarding the development of the embryos, most evident in *C. robusta*. The embryos seem first to develop eyes, this being accompanied and followed by the development of the long cone of mouthparts and finally by the acquisition of a complete segmentation of pereon, the embryos look like pranizae with swollen pereons in the younger developmental stages. The most developed embryos of *C. robusta* measured on average 2.24±0.07 mm (Table 12) and were probably ready to leave the female. Six of the seven females of *C. abyssorum* contained very young embryos, only in one female was found more developed embryos of an average length of 1.61±0.08 mm, having eyes, long mouthparts and being completely segmented (Table 12). They were probably about being ready to leave the female. If the estimated average length of respectively 2.24 mm for *C. robusta* and 1.61 mm for *C. abyssorum* are representative for the size by which the pranizae leave the female, then this indicates that the average length of a newly released praniza in relation to the average length of the female is bigger in *C. abyssorum* (1.61 mm/3.6 mm = 0.45) (Tables 10 and 12) than in *C. robusta* (2.24 mm/5.7 mm = 0.39) (Tables 9 and 12). Accordingly, a female *C. abyssorum* produces fewer but bigger pranizae than a female *C. robusta*.

Digestive caeca indices of males

According to Upton (1987a: 681-682) a distinction between recently moulted adult males and males of the previous generation of *Paragnathia formica* is easily made "since the pereons of the former were greatly distended by the large digestive caeca, whilst those of the latter appeared shrunken and hollow due to the depletion of caecal food reserves". On this basis, an index score with three stages of the digestive caeca was developed for *C. robusta* and *C. abyssorum*. To examine the existence of a seasonal difference the results are shown for each sampling month (Fig. 5). In Fig. 5 the number of dead males found in each sampling month is also included. The number of sponges examined varies between months and this is reflected in the number of gnathiids obtained. Thus, the majority of the males were obtained in September, this being most pronounced for *C. robusta*. Nearly equal numbers of males of digestive caeca Stage I and II were present in September of *C. robusta* while a trend towards a larger representation of Stage I males is seen in the July and especially in the October samples. Only one male of Stage III was found in September. Dead males are present in both September and October, the proportion of these in relation to the total number of males per month showing a trend towards an increase from September to October. The two adult males collected in respectively June (the Ingolf Expedition) and August (the R/V *Polarstern* cruise ARK VII/2 collection) were both of Stage I (Fig. 5A).

In *C. abyssorum* a greater part of the adult males are of digestive caeca Stage I in September as compared with the October specimens. Only one male of Stage III was present in both sampling months and the representation



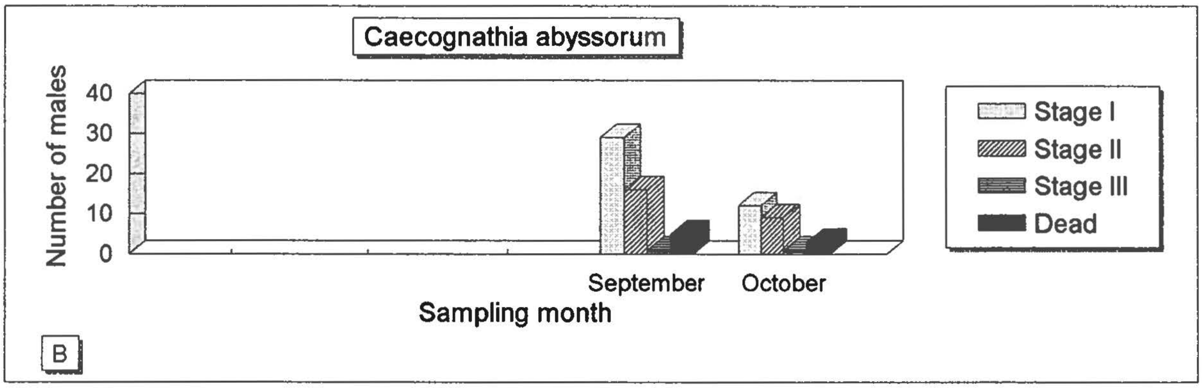


Fig. 5. Digestive caeca index of adult males of respectively *Caecognathia robusta* (A) and *C. abyssorum* (B). Number of males of each of the three digestive caeca stages as well as of dead males of each sampling month are shown. Only intact males are included in the index score.

of dead males is almost the same in September as in October, only slightly increasing in October in relation to the total number of males per month (Fig. 5B).

Reproductive activity

The reproductive activity of the adult males of *Caecognathia robusta* and *C. abyssorum* of digestive caeca Stage I and II (the two stages that were numerically best represented) was examined by estimating the percentage representation of single males and of males together with female(s) of different reproductive stages in the different sampling periods (Figs 6 and 7). As only a small number of males of *C. robusta* were collected in June, July and August these are shown together. Comparing the reproductive activity of the adult males of Stage I and II of *C. robusta* in Fig. 6 shows that single males as well as males together with pranizae or mature females are found in all three sampling periods for both digestive caeca stages of males, the only exception being the lack of Stage II males together with pranizae in October. For digestive caeca Stage I males the part of single males is increasing from June, July & August through September to October indicating a settling and moulting of male pranizae into adult males during this period. Sixty percent of the Stage I males and 40% of the Stage II males were however found together with ovigerous females in the June, July & August period demonstrating that reproduction is well under way at that time.

Single males of *C. abyssorum* as well as males together with female pranizae or mature females are, as for *C. robusta*, present in both sampling months for males of digestive caeca Stage I and II (Fig. 7).

The one male of digestive caeca Stage III of *C. robusta* in the September samples (Fig. 5A) was single, and the two males of Stage III of *C. abyssorum* (Fig. 5B) were respectively a single male (September) and a male with a praniza (October) (males not included in Figs 6 and 7).

Discussion

Identifications of the gnathiids

Hansen (1916) noted that the degree of granulation and number of spines on head and thorax of the adult males of *Caecognathia robusta* vary, and this variation is also seen in the present material. The pranizae found together with adult males (*C. robusta* or *C. abyssorum*) were all as big as or bigger than the male (Tables 9 and 10) and are regarded as being of third stage going to moult to mature females. It has to be added that only four species of gnathiids have been studied in more detail regarding life history. However, three praniza stages have been reported for *Gnathia maxillaris* (Mouchet 1928), *Paragnathia formica* (Stoll 1962; Upton 1987a), *Caecognathia calva* (Wägele 1987, 1988) and *C. abyssorum* (Klitgaard 1991) and seem to be the general rule in the family. Therefore it seems justified to assume that three praniza stages exist in *C. robusta*, too. The pranizae as well as the adult females found together with a male are evaluated as belonging to the same species as the male. This seems to be justified by the fact that only one species, *C. robusta*, judging from the males, was found in the preoscular cavities of *Geodia mesotriaena*, and mainly two species, *C. robusta* and *C. abyssorum*, representing very different size categories (Tables 9 and 10) were present in *Hexadella dedritifera*. The two finds of *C. hirsuta* in *H. dedritifera* demonstrate a very infrequent presence of this gnathiid in the sponge.

The majority of the pranizae present in *Hexadella dedritifera* were found singly (Tables 6 and 7), making their identity uncertain, most likely, however, they belong to *Caecognathia robusta* or *C. abyssorum*. Descriptions of the pranizae are seldom included in the taxonomical literature of the Gnathiidae, as the pranizae of different species are very similar in their morphology, making it difficult to find reliable characters to be used for their identification to species level. Exceptions are the work by Cals (1978) and Wägele (1987). Only few notes exist on the morphology of the pranizae of North Atlantic and Arctic species of Gnathiidae (Sars 1885; Hansen 1916; Monod 1926). The examination of the character mentioned by Monod (1926), that is the number of flagellar articles of antenna 2 (Table 11), demonstrates the insufficiency of the existing descriptions of the pranizae of *C. robusta* and *C. abyssorum*, and that the identity of the single pranizae in *Hexadella dedritifera* cannot be resolved at present.

Comparing the length frequencies of the pranizae found singly in *H. dedritifera* (Fig. 4) with the sizes of respectively the first segmented praniza stage and the third swollen praniza stage of *C. robusta* and *C. abyssorum*, respectively 2.24±0.07 and 1.61±0.08 mm (Table 12) and 6.5±0.84 mm and 4.3±0.47 mm (Tables 9 and 10), the most probable intuitive suggestions are that the segmented pranizae measuring between 1.9 and 2.5 mm are second stage pranizae of *C. abyssorum* while the diffuse group of segmented pranizae being about 4.9 mm in total length are too big to be of this species and most likely are third stage pranizae of *C. robusta*. However, whether the peak of segmented pranizae about 3.1-3.3 mm are second stage pranizae of *C. robusta* or third stage pranizae of *C. abyssorum* cannot be solved at present. Swollen pranizae being more than 5.0 mm in total length are too big to be *C. abyssorum* and therefore most likely are third stage pranizae of *C. robusta*. The difficulties arise when considering the two peaks about respectively 2.4-2.7 mm and 3.9 mm. Whether these two peaks represent second and third stage pranizae of *C. abyssorum* or first and second stage pranizae of *C. robusta* cannot be decided for the moment.

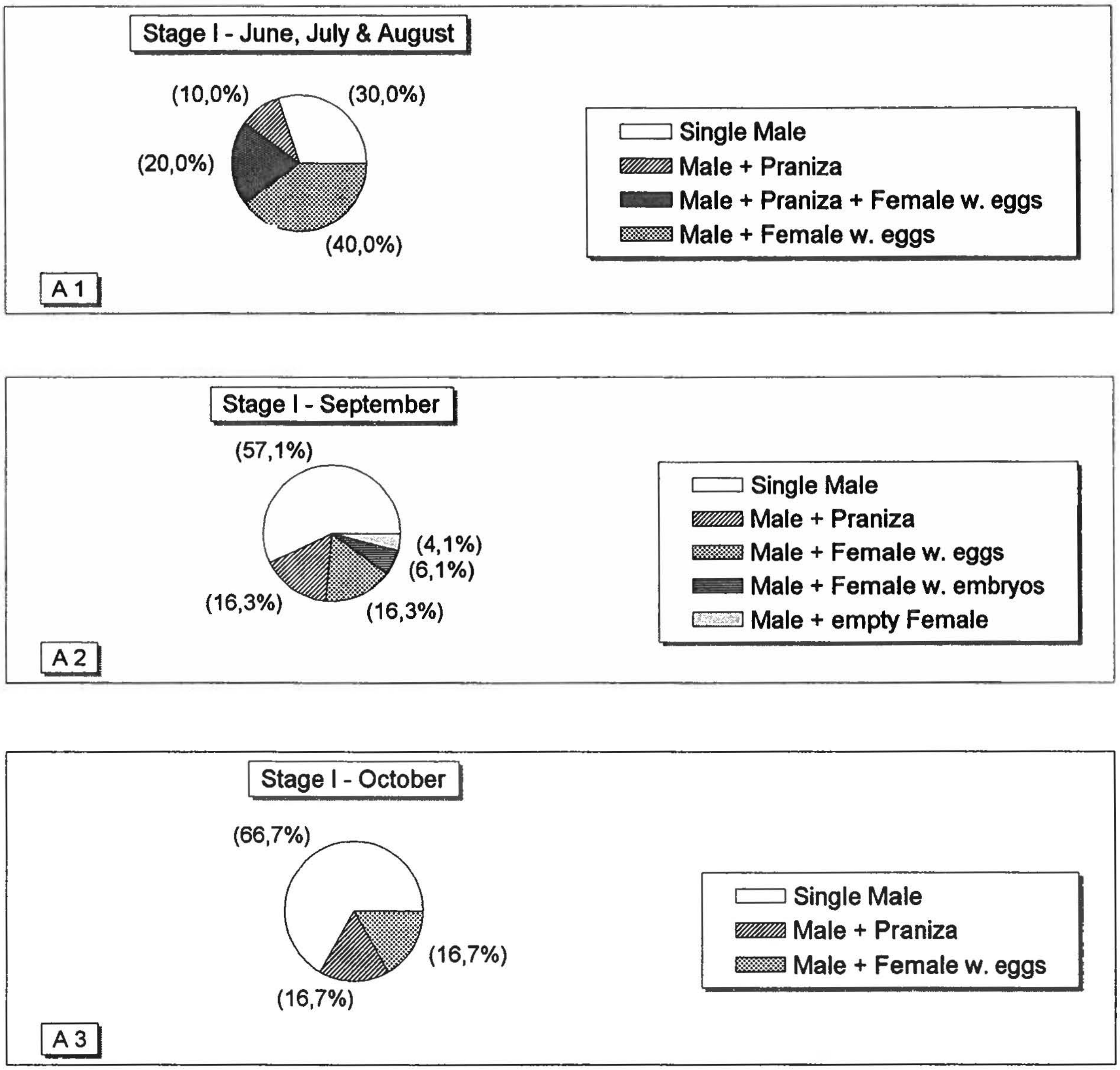


Fig. 6. Reproductive activity of adult males of *Caecognathia robusta*. The activity is indicated for each sampling period as the percentage of the males of digestive caeca index I (A1-A3) or II (B1-B3) being present singly or together with either a third stage praniza or a mature female or both, the female being ovigerous, filled with embryos or empty. Only intact males are included in the estimations.

Variations in size of the adults of *Caecognathia robusta* and *C. abyssorum*

Hansen (1916) noted that *C. robusta* is very variable regarding the size of the adult males. He examined eight of the ten males, collected during the Norwegian North-Atlantic Expedition at Svalbard and described by Sars (1879, 1885), and found a variation of the total length between 4.3 and 6.6 mm. A similar variation of the size of the adult males and females of *C. robusta* is found in the present collection (Table 9). The variation seems not to be related to the geographical distribution of the species as the sizes overlap in the different investigated areas, being respectively 7.5 mm (♂) in the Fram Strait, 4.1-7.9 mm (♂) and 4.3-7.1 mm (♀) in the Denmark Strait, 5.1-7.5 mm (♂) and 5.0-7.1 mm (♀) north of Iceland, 8.1 mm (♂) and 6.4 mm (♀) at 1070 m W of Iceland and 5.1 mm (♂) SE of the Faroe Islands (Table 9). However, from some localities only few specimens were measured. Also Barthel & Brandt (1995) measured the total length of the adults of *C. robusta* collected at NE Greenland, the sizes varying between 5.5 and 9.0 mm (♂) and 4.5 and 7.5 mm (♀).

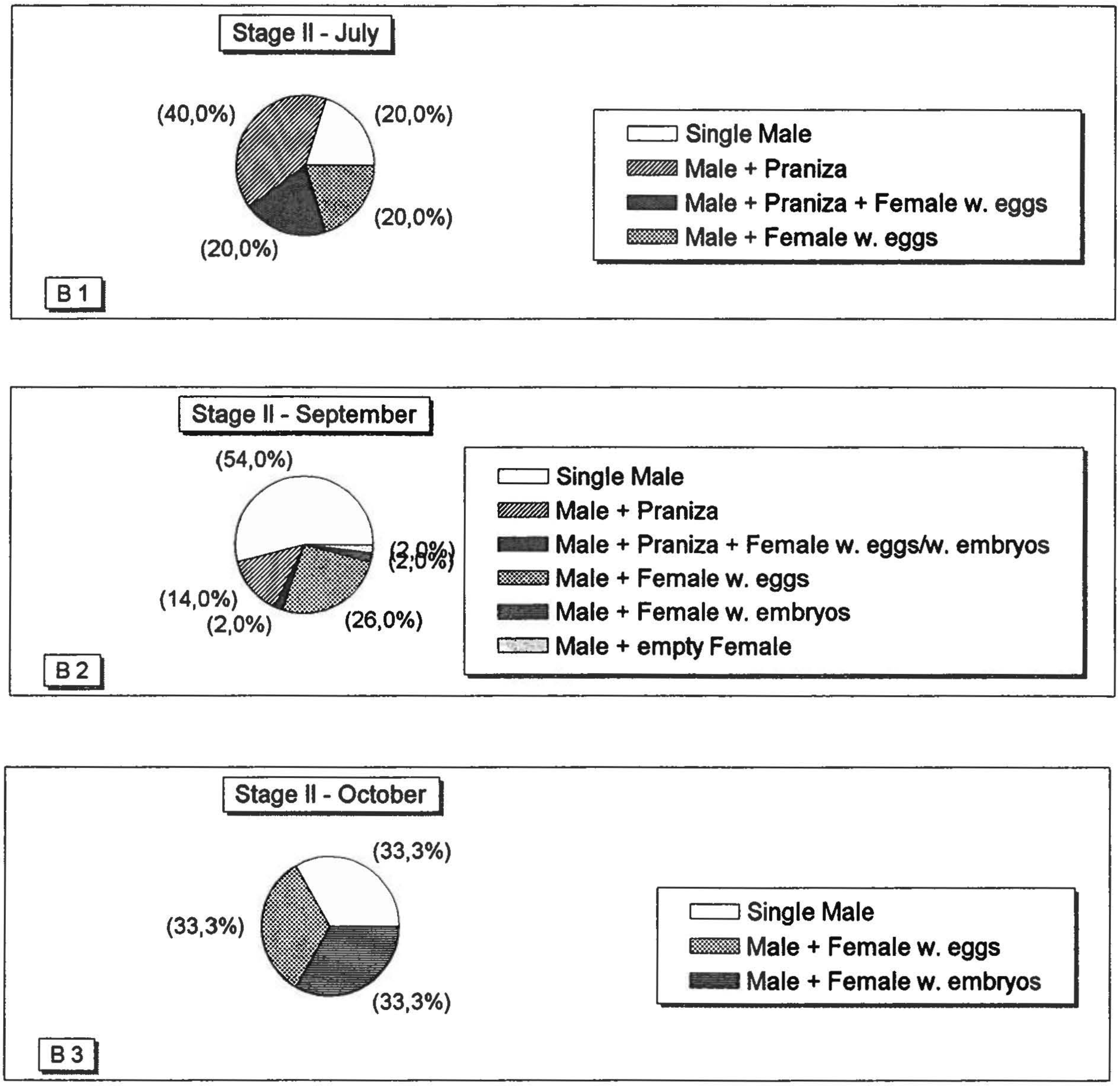


Fig. 6. continued

The previously reported size of *C. abyssorum* varies between 2.5 and 3.5 mm, the smallest specimen being a male collected west of Ireland (Sars 1899; Hansen 1916; Monod 1926). A marked difference in size was observed between the adults of *C. abyssorum* of the present collection and the adults sampled at the Faroe Islands (Klitgaard 1991) (Table 10).

Smith (1904) reported a variation in size of adult *G. maxillaris* between 1 and 8 mm (♂) and 1 and 7 mm (♀), this variation being even more extreme than the one observed in *C. robusta* in the present investigation. Smith explained this difference as being dependent on the size of the praniza that moults into an adult. Some degree of variation of the total length can be expected within each praniza stage depending on the distension of the pereon. Whether this is a sufficient explanation for the extreme variation observed by Smith (1904) or if more than one species were present in Smith's material is not known. A variation in the total length of the swollen third stage pranizae was observed in the present material of *C. robusta* and *C. abyssorum* (Tables 9 and 10). However, the existence of a relation between the size of the moulting praniza and the resulting adult needs to be examined.

Hexadella dedritifera is only few millimeter thick and

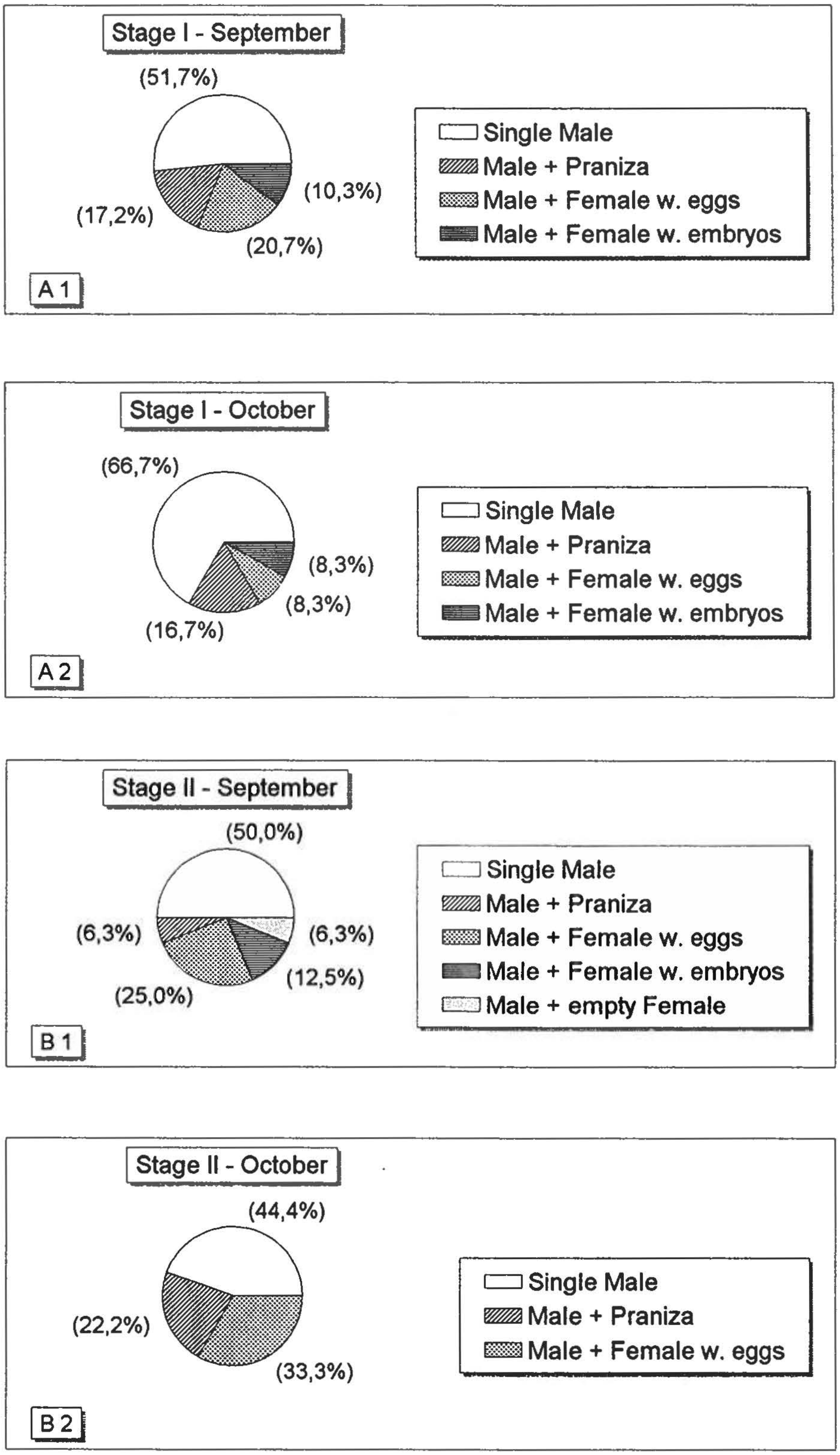


Fig. 7. As in Fig. 6 only for *Caecognathia abyssorum*. (A1, A2) = males of digestive caeca index I, and (B1, B2) = males of digestive caeca index II collected in September or October.

is, due to the lack of a skeleton, a rather soft sponge. The general impression is that the lacunae used by the gnathiids are not as well-defined as the more massive preoscular cavities of *G. mesotriaena*, and also that the lacunae of *H. dedritifera* in average are of a smaller volume than the preoscular cavities, leaving less space for the gnathiids. The found significant difference between the means of the adult males of *C. robusta* inhabiting the two sponge species might indicate a tendency towards a host induced speciation as has been suggested for tropical sponge-dwelling alpheid shrimps (Duffy 1996). A thorough morphological examination of adult males from different habitats is necessary to develop this idea further.

Distribution of *Caecognathia robusta* and *C. abyssorum* in relation to hydrography

Bottom temperature and salinity were recorded on most of the stations (Table 3) and the bottom temperature on a number of the previous records of both species (Table 2). Comparing the known distribution of *Caecognathia robusta* (Fig. 1, Tables 2 and 3) with the definitions of water masses in Blindheim et al. (1996), it appears that *C. robusta* is distributed in Arctic Intermediate Waters north of the Greenland-Iceland-Faroe Ridge, and primarily in the Iceland Sea Arctic Intermediate Water (Temperature < 2 °C; Salinity 34.7-34.9) in the Denmark Strait and at the BIOICE stations north of Iceland (salinity for BIOICE Stns 2758 and 2769, Table 2, is 34.88 and 34.86 respectively). Iceland Sea Arctic Intermediate Water is also found north of the Denmark Strait in the East Greenland Current below the Polar Water, as is the East Greenland Current Intermediate Water (Temperature 0-2 °C; Salinity 34.9-35.0) (Buch 1991; Blindheim et al. 1996). Accordingly, the records of *C. robusta* at 550 m in the Fram Strait, in the depth interval 777-840 m at NE-Greenland and at 314 m off East Greenland in the Scoresbysund area are in these watermasses. The single record at BIOFAR St.no. 041 SE of the Faroe Islands in the Faroe-Shetland Channel at 780 m was probably in the Norwegian Sea Arctic Intermediate Water (-0.5 < Temperature < +0.5 °C; 34.87 < Salinity < 34.90) (Blindheim et al. 1996). The knowledge of the physical oceanography of Baffin Bay is limited, but from the few existing data the single specimen of *C. robusta* was collected at a depth (208 m) probably dominated by cold water with a temperature below 0 °C (Buch 1991). The records of *C. robusta* west of Svalbard and between Finmark and Bjørnøya are, judging from the known depths and temperatures (Table 2), in the cooled Atlantic Water of the Norwegian Atlantic Current (Tchernia 1980), the Atlantic Water in the Nordic Seas being defined as water with a temperature above 0 °C and salinities above 35 (Blindheim et al. 1996). Similarly, the single record north of Svalbard at 1000 m as well as the two records in the Arctic Sea (the Nansen Basin) from depths between 300 and 360 m (Table 2) are probably in the cooled Atlantic Water (Tchernia 1980). No depth and no temperature are reported in Gurjanova (1933) for the station in the Barents Sea (Table 2). The presence of *C. robusta* at *Ingolf* Stns 9 and 90 west of Iceland at temperatures of respectively 5.8 and 4.4 °C is remarkable being the two only records of this species south of the Greenland-Iceland-Faroe Ridge in warmer Atlantic Water. However, only one male was found on *Ingolf* St.no. 9 and only one male and two females on *Ingolf* St.no. 90 (Tables 2 and 5). Presuming that the two Atlantic records belong to the same species as the cold water specimens, the specimen of *Ingolf* St.no. 9 being identified by H. J. Hansen (1916) and the identity of the specimens of *Ingolf* St.no. 90 being checked by N. L. Bruce, the existing data demonstrate that *C. robusta* is primarily occurring north of the Greenland-Iceland-Faroe Ridge in the cold Arctic Intermediate Waters as well as in the cold water north of the sill in the Davis Strait. The species can, however, also be found in Atlantic Water respectively in the cooled Atlantic Water in the northern continuation of the Norwegian Atlantic Current along the westcoast of Bjørnøya and Svalbard, but also south of the Greenland-Iceland-Faroe Ridge in warmer Atlantic Water, but only infrequently.

Caecognathia abyssorum has primarily been found in the Atlantic Water of the North Atlantic Current and the two main branches of this current; the Norwegian Atlantic Current along the westcoast of Norway and the Irminger Current south and west of Iceland (Johannessen 1986) (Fig. 2). Exceptions to this distribution pattern are the deepest stations at the Faroe Islands, at 400-500 m, influenced by an admixture of colder Arctic Intermediate Water (Westerberg 1990). No temperature is reported for the R/V *Thor* station east of Iceland at 130 m (Table 2), but it is probably influenced by the North Icelandic Winter Water (2 < Temperature < 3 °C; 34.6 < Salinity < 34.9) of the eastern continuation of the East Icelandic Current (Malmberg & Kristmannsson 1992; Blindheim et al. 1996). The record at Rathbone Island, in the Scoresbysund area (Table 2), is reported as being at either 175 or 300 m (Hansen 1916; Stephensen 1943). The specimen was probably collected at 300 m in the Iceland Sea Arctic Intermediate Water and not at 175 m in the Polarwater of the East Greenland Current (Buch 1991) as *C. abyssorum* has not been recorded at negative temperatures at any other localities. All records in the Denmark Strait are similarly situated in the Iceland Sea Arctic Intermediate Water. *C. abyssorum* has also been collected on top of the sill in the central part of the Davis Strait (Fig. 2) at a depth (176 m) probably dominated by the Atlantic Water of the Irminger Current (Buch 1991).

In conclusion *C. abyssorum* is mainly an Atlantic species occurring south of the Greenland-Iceland-Faroe Ridge and along the westcoast of Norway. The present data demonstrate, however, that it can also be found in cold Arctic Intermediate Water, but most probably not in a watermass of a negative temperature. Thus, *C. abyssorum* is only found co-occurring with the coldwater species *C. robusta* in the Iceland Sea Arctic Intermediate Water of the Denmark Strait. Both species are also found at *Ingolf* St.no. 9 west of Iceland in Atlantic Water (Table 2), which is, however, probably an infrequent occurrence regarding *C. robusta*.

The habitats of gnathiids

Most gnathiids seem to inhabit cavities (Holdich & Harrison 1980; Kussakin & Vasina 1980, 1982; Nunomura 1981, 1982; Poore 1981; Davies 1982; Kensley & Snelgrove 1987; Müller 1988, 1989a, 1989b, 1991, 1993a, 1993b; Wägele 1988; Klitgaard 1991; Jensen & Frederiksen 1992; Cohen & Poore 1994; Barthel & Brandt 1995). The only species that has been observed actively digging is the littoral *Paragnathia formica*, in which the males dig galleries in estuarine mudbanks (Monod 1926; Naylor 1972; Upton 1987a). It is possible however that other gnathiid species found in sand-mud substrates have a similar habit.

Caecognathia robusta has previously only few times been recorded associated with sponges, respectively with "a calcareous sponge" collected during the Ingolf Expedition (unknown station) (Table 2) (Hansen 1916) (identified to *Grantia capillosa* (Schmidt, 1862), l.c. O.S. Tendal), and with *Sycon* sp. (Calcarea) collected north of Iceland and with *Geodia mesotriaena* collected at NE-Greenland (Table 2) (Barthel & Brandt 1995). The first record of an association with *G. mesotriaena* is, however, by Hentschel (1929) who in the original description of this sponge species noted the presence of an isopod in the preoscular cavity of the holotype as well as in one additional examined specimen. An adult male of *C. robusta* was found by the present author in the preoscular cavity of one of Hentschel's specimens labelled "co-type". The holotype had previously been cut in four pieces and the preoscular cavity was empty, and nothing was found in the jar of the specimen. Thus, the record is included in Table 2 as 1-2 ♂.

Similarly, only few previous reports of sponge associations exist for *C. abyssorum*, respectively with *Halichondria tenuiderma* southwest of Iceland (St.no. 81 of the Ingolf Expedition, Table 2) (Hansen 1916), and with "a sponge" collected in the Hjeltefjord, Norway (Monod 1926). In addition the present author noticed a note on a label in the jar with the male collected at Rathbone Island, East Greenland (Table 2) saying that the specimen had been found "in a sponge", this information not being included in any of the examined expedition reports. The hitherto largest number of *C. abyssorum* associated with sponges was found at the Faroe Islands (Table 2) (Klitgaard 1991). In the Faroese investigation *C. abyssorum* was found in two different habitats representing sponges of two different morphological groups; in the spicule "fur" on the surface of large, massive sponges (*Stryphnus ponderosus* and *Stelletta normani*), and in the canals connecting the incurrent and excurrent sides of foliaceous or funnel-shaped sponges (*Tragosia infundibuliformis*, *Axinella arctica* and *Phakellia robusta*). In addition *C. abyssorum* was at the Faroe Islands also found in small crevices in dead coral rubble of *Lophelia pertusa* (Jensen & Frederiksen 1992).

The results of the present investigation as well as the previous records show that the generally accepted concept of adult, reproducing gnathiids (Seed 1979; Holdich & Harrison 1980; Brandt & Wägele 1991; Cohen & Poore 1994), being found in some kind of protected cavity also seems to apply for *C. robusta* and *C. abyssorum*. As described for *Paragnathia formica* in Britain and northern France (Monod 1926; Naylor 1972; Upton 1987a), *Caecognathia calva* in the Antarctic (Wägele 1988) and *C. agwillisi* (Seed, 1979) in Victoria, Australia (Seed 1979) also *C. robusta* and *C. abyssorum* were in the present investigation found in cavities with a male positioned at the entrance, probably ready to project the mandibles to deter potential invaders or predators. So positioned the pereon and pleon of the male is protected inside the cavity and only the very broad and heavily chitinized head with the large mandibles protrudes from the opening. A positive correlation was found between the diameter of inhabited excurrent openings in *Geodia mesotriaena* and the maximum width of the heads of the males of *C. robusta*. Thus, the males seem to choose cavities where their heads fit as "plugs" in the excurrent openings (Pl. I, A and Fig. 3), these cavities being defended most efficiently by the males. Likewise Barthel & Brandt (1995) only found *C. robusta* in specimens of *G. mesotriaena* with excurrent openings with diameters between 1 and 4 mm. Another purpose of this position is probably to capture approaching female pranizae with the mandibles and drag them into the cavity as described for *Paragnathia formica* (Upton 1987a). In fact, some of the males of both *C. robusta* and *C. abyssorum* were holding on to a praniza, which probably had just been captured (Pl. I, E, F). The position of the males in the entrance of the preoscular cavity in *G. mesotriaena* might explain why some of the males had injured mandibles or heads or even had been decapitated during sampling.

Hexadella dedritifera seems to be a commonly used substratum of the reproducing adults of both *C. abyssorum* and *C. robusta*, as well as of pranizae during the digestion periods and moulting events. The small number of segmented pranizae compared to swollen pranizae (Fig. 4A, B) is to be expected as these probably only stay hidden in the sponge for a short period before they start searching for a fish host. In contrast only mature adults or pranizae of third stage of *C. robusta* were present in the preoscular cavities of *G. mesotriaena*, but not mature adults of *C. abyssorum* nor first or second praniza stages of neither species. Housing shortage cannot be the reason, as 74.6% of the excurrent openings with diameters between 0.30 and 0.49 mm and 95.7% of the remaining excurrent openings were unoccupied (Fig. 3). Part of the explanation could be that *C. abyssorum*, being primarily an Atlantic species, is unable to colonize *G. mesotriaena* living in a watermass of negative temperature (Table 3).

A tendency towards a habitat division was observed between *C. robusta* and *C. abyssorum* in respectively free living and episponge specimens of *Hexadella dedritifera* (Tables 6 and 7). As all samples from the Denmark Strait originate from the Iceland Sea Arctic Intermediate Water (Blindheim et al. 1996) (Table 3), different temperature preferences are not likely to be an explanation. The observed tendency may, however, be caused by a similar gregarious settlement of pranizae in areas where adult males already are established, as reported for *Paragnathia formica* (Upton 1987b), thereby perhaps reducing the settlement of pranizae of other species.

The very low degree of colonization of gnathiids in species of *Thenea* is remarkable (Tables 3 and 8). An examination of the total associated fauna of *T. levis* and *T. valdiviae* at the Faroe Islands demonstrated the presence of a large number of associated species in the spicule "fur" of both *Thenea* species, including especially species of nematodes, polychaetes and bryozoans. However, only few crustaceans and no gnathiids were found (Klitgaard 1995). One explanation probably accounting for the lack of *C. abyssorum* is that a large number of the specimens of all four *Thenea* species were sampled at negative temperatures. Some specimens came, however, from Atlantic Water of higher temperature and would appear suitable for colonization of *C. abyssorum*. Likewise *C. robusta* would have been expected to inhabit a larger number of osculae in specimens from cold water. There is therefore at the moment no obvious explanation.

"Harem" formation

Knowledge of biology and life history of the adult gnathiids is limited and fragmentary. Gnathiid males collecting and living in "harems" are often referred to and this behaviour seems to be regarded as a general rule in the family (Brandt & Wägele 1991; Cohen & Poore 1994; Barthel & Brandt 1995). The phenomenon has, however, only been observed in three species. *Paragnathia formica* is the best documented "harem" former (Monod 1926; Naylor 1972; Upton 1987a), up to 25 females having been observed together with one male in a burrow (Upton 1987a, b). Mouchet (1928) mentions briefly the observation of assemblings of adults as well as of pranizae of different stages in the intertidal *Gnathia maxillaris* in northwestern France. Wägele (1988) reports the frequent presence of "harems", consisting of one male together with up to 43 females or immature specimens of *Caecognathia calva*, inhabiting the oscular cavities of small hexactinellid sponges in the Antarctic. In contrast, Seed (1979: 57) emphasizes that none of the adult males of the littoral Australian *C. agwillisi*, were found together with more than two females "one older and gravid, or post-partum and the other recently metamorphosed or even still in the late juvenile state". The formation of "harems" has also been suggested for *C. abyssorum* at the Faroe Islands, where most of the adult males were found together with a number of adult females and/or pranizae (Klitgaard 1991). Jensen & Frederiksen (1992) found adult females of *C. abyssorum* to be more than five times as frequent as adult males in crevices in the scleractinian coral *Lophelia pertusa* from the Faroe Islands. In the present investigation no tendency at all was found for "harem" formation in *C. abyssorum*, as no adult male was found together with more than one female (third stage praniza or mature female) (Tables 6 and 7). Barthel & Brandt (1995) consider *C. robusta* to be a "harem" former. They found four females together with one male in a preoscular cavity of one specimen of *G. mesotriaena* at NE Greenland, and five females in company with a male in a *G. mesotriaena* collected north of Iceland. These two records can be interpreted as kinds of "harems" being, however, of infrequent occurrence and of much smaller size than the "harems" reported for *Paragnathia formica* and *Caecognathia calva* (Upton 1987a, b; Wägele 1988). The majority of the preoscular cavities examined by Barthel & Brandt (1995) contained single males of *C. robusta* (26.9%), pairs (57.7%) or one male together with two females (11.5%). To this can be added the report by Hansen (1916) of one male of *C. robusta* found together with two mature females and a praniza in a small vase-shaped, calcareous sponge (Table 2).

No more than one female was found together with any of the adult males of *C. robusta* in the specimens of free living *H. dedritifera* (Table 6) and in the osculae of *Thenea valdiviae* (Table 8). Adult males were, however, occasionally found in company with two or three females in a preoscular cavity in *Geodia mesotriaena* (Table 5). The present author suggests that the number of females found together with a male (*C. robusta* or *C. abyssorum*) depends on the volume of the cavity. As mentioned before the general impression is that the lacunae used by the gnathiids in *H. dedritifera* generally were smaller and not as well-defined as the preoscular cavities of *G. mesotriaena*, not leaving room for more than one female together with a male. The volume of the preoscular cavities of *G. mesotriaena* was variable, and some of the males of *C. robusta* were found in small cavities just big enough for the male, but without space for a female (Pl. I, C). Most of the cavities were of a volume giving room for a pair (Pl. I, B) and a small number of the cavities were bigger, with space for two or three females in addition to a male (Pl. I, D).

Digestive caeca index

To get an impression of the age structure of *Caecognathia robusta* and *C. abyssorum* in the present material an index score of the digestive caeca was developed (Fig. 5A, B). Following the concepts of Upton (1987a) Stage I males are recently moulted, Stage II males are older males from same generation as the Stage I males and Stage III males are from the previous generation, as are the dead males. The majority of the present material was collected in September, but it is, however, evident from Fig. 5A that newly moulted adult males of *C. robusta* were found in all samples from June to October. About fifty percent of the adult males of *C. robusta* are of Stage

II in July and September having depleted some of the caecal food reserves and inferring that male pranizae must have been settling during the spring months or earlier. Only one male of digestive caeca Stage III and very few dead males were found of *C. robusta*.

In *C. abyssorum* recently moulted adult males (digestive caeca Stage I) are dominating in both September and October, this being most pronounced in September (Fig. 5B). The simultaneous marked representation of males of digestive caeca Stage II in both sampling months demonstrates, as for *C. robusta*, that a settling of male pranizae must have been happening during the previous spring and summer months. The representation of males of digestive caeca Stage III and dead males is somewhat more marked than in *C. robusta* being, however, not extensive.

Brood size

The average number of embryos per brood is about 3.5 times as many in *C. robusta* as in *C. abyssorum* (Table 12). Wägele (1988) reports a production of 129.3 ±28.4 eggs on average per female of *C. calva*, and Upton (1987a) describes the release of broods of up to 140 pranizae for *Paragnathia formica*. The length of the females are about 6 mm in *C. calva* (Wägele 1988) and 4-5 mm in *P. formica* (Upton 1987a). *Caecognathia calva* is of a comparable length to *C. robusta*, while the length of *P. formica* overlaps the length of both *C. robusta* and *C. abyssorum* (Tables 9 and 10). Both species are, however, producing broods of a size comparable to *C. robusta*, while *C. abyssorum* produces broods of averagely 33 embryos per female (Table 12). The average length of late stage embryos in relation to the average length of the females of *C. abyssorum* and *C. robusta* can be compared to the equivalent values of *C. calva* (1.5 mm/6.0 mm = 0.25) (Wägele 1988) and of *P. formica* (1.0 mm/4.5 mm = 0.22) (Upton 1987a): The two "harem" forming species appear to produce relatively smaller first pranizae than *C. robusta* and *C. abyssorum*. Wägele (1987) observed in *C. calva* that an immature, passive earlier stage sometimes is found. This immature stage has a gut swollen with a transparent liquid and the cuticle of the central pereonites is stretched. After excretion of the fluid, the gut is barely visible, the pereon is fully segmented and the juvenile becomes an active first praniza that is shorter than the immature praniza. However, the most developed embryos of *C. robusta* and *C. abyssorum* did not have a stretched pereon, but were completely segmented, wherefore a comparison with the length of the newly released first pranizae of *C. calva* and *Paragnathia formica* seems justified.

According to previous descriptions of the adult females of *C. robusta* (Sars 1885; Hansen 1916), they are extremely thick, considerably thicker than in *C. abyssorum*. Similarly females found singly in preoscular cavities in *Geodia mesotriaena* (Table 5) all filled the entire cavity, and in a number of the pairs present in *G. mesotriaena* the female filled up most of the cavity, leaving restricted room for the male (Pl. I, B). As the females of *C. robusta* produce the same number of embryos as reported for "harem" forming species of Gnathiidae, the embryos are, however, bigger, this causes the females to appear distended.

Reproductive activity

Barthel & Brandt (1995) mention that most of the females collected in July at NE-Greenland contained eggs as well as the females collected north of Iceland in the beginning of August. The data of these authors show that males together with pranizae as well as males together with mature females were present in the examined sponges in July. In the present investigation single males and males together with pranizae or mature females of *Caecognathia robusta* were present in both June, July & August, September and October for both digestive stage I and II of males (Fig. 6). The presence of Stage I males with female pranizae in September as well as in October, the proportion of these not decreasing, points to a continuing reproduction. In September Stage I males are found together with females containing embryos or with empty females, inferring that an adult male is able to survive for long periods on the caecal food reserves, as a total female reproductive sequence from moulting into an adult female through development and release of the brood can be completed with the male still having two large digestive caeca. Having this in mind then two possibilities can be suggested for the data of the Stage II males. Either these have been very unsuccessful in capturing a female praniza, the males having depleted part of the caecal food reserves before succeeding, or the males have survived one female reproductive sequence and are ready to start the next one (single males) or are already in progress with the next sequence (males with pranizae or mature females). The three males of digestive caeca Stage II of *C. robusta* in October were equally divided in one male probably ready to start a female reproductive sequence (single male) and two males respectively in the middle and in the end of a sequence (male with an ovigerous female and male with a female with embryos).

For *C. abyssorum*, it can be inferred that reproduction must have been in progress for a while in September as males of both digestive caeca stage I and II were present together with females with embryos, and further that the reproduction is not showing any sign of being decreasing in October as about 20% of both digestive caeca stages of males were found together with a praniza (Fig. 7). That Stage I males were found together with females with embryos demonstrates, as for *C. robusta*, that the males must be able to survive for long periods on the caecal food reserves. In addition the present results demonstrate the possibility that the males of *C. abyssorum*, as also inferred for the males of *C. robusta*, complete two or more female reproductive sequences before having depleted the caecal food reserves. The Stage III male of *C. abyssorum* present in October (Fig. 5B) was found together with a praniza. This male appeared totally hollow without any remaining food reserves, and it is doubtful whether the male would have been able to complete a further female reproductive sequence. However, if the female is fertilized before the male dies, then the sequence can possibly be completed, the female being, however, more vulnerable due to the lack of a defender of the cavity. This is perhaps the explanation for the mature females of *C. robusta* as well as of *C. abyssorum* found singly in *Geodia mesotrianea* and *Hexadella dedritifera* (Tables 5, 6 and 7). These were all either ovigerous or contained embryos or were already empty showing that a male had been present previously. That low numbers of empty females of both gnathiid species were found (Figs 6 and 7) is probably owing to these being ejected from the cavity by the male after having released the brood as described for *Paragnathia formica* (Upton 1987a).

Seasonality and reproductive strategy

A seasonal reproductive activity has been reported for *Paragnathia formica* (Upton 1987a), *Caecognathia calva* (Wägele 1988) and *C. abyssorum* (Klitgaard 1991). At the Faroe Islands adult females of *C. abyssorum* with eggs or embryos or empty females were only present in samples from May-June and the reproduction is expected to start in spring and to end about July-August (Klitgaard 1991). In the littoral *Paragnathia formica* breeding is confined to the warmer summer months, the total lifespan being reported as about one year for females and up to two years for males (Upton 1987a). The Antarctic *Caecognathia calva* was in laboratory experiments kept at temperatures between 0 and -1 °C, and observed to release broods between February and May, and the lifespan recorded to be respectively four to five years for the females and up to more than six years for the males (Wägele 1988).

Seasonal reproduction is expected to be triggered by variations in the environment or in the accessibility of food. *C. robusta* has its main distribution in the cold Arctic Intermediate Waters north of the Greenland-Iceland-Faroe Ridge and the present material of *C. abyssorum* was collected in the Iceland Sea Arctic Intermediate Water in the Denmark Strait, these water masses showing only minor variations in temperature throughout the year.

Since food is only ingested by the haematophagous praniza stages, these are dependent of the accessibility of suitable fish hosts. The fish host of pranizae has only infrequently been identified, and similarly the hosts of the pranizae of *C. robusta* and *C. abyssorum* are not known at present. As reported for the littoral *Paragnathia formica* in northern France (Monod 1926), the intertidal *Gnathia maxillaris* in Wales, U.K. (Davies 1982) and the bathyal *Caecognathia calva* in the Antarctic (Wägele 1988; Rokicki et al. 1992) the hosts of *C. robusta* and *C. abyssorum* probably include several species of fish. Fish species regularly caught in the Denmark Strait include *Boreogadus saida* (Lepechin, 1774), *Mallotus villosus* (Müller, 1777), *Sebastes marinus* (L., 1758), *S. mentella* Travin, 1951, *Anarhichas lupus* L., 1758, *Reinhardtius hippoglossoides* (Walbaum, 1792), *Hippoglossoides platessoides* (Fabricius, 1787), *Lycodes* sp., *Triglops pingeli* Reinhardt, 1832 and *Benthosema glaciale* (Reinhardt, 1837) (P. Kanneworff pers.comm.). At least some of these fish species, for which the biology is known in some detail, are migrating (B. Muus pers.comm.), and if they constitute hosts for the pranizae of *Caecognathia robusta* and *C. abyssorum* this would introduce a seasonal component in the life-cycle of the gnathiid species. A seasonal variation in the reproductive intensity has been reported for continuously reproducing deep-sea asellote isopods, which is suggested to be synchronized with the seasonal deposition of organic detritus (Harrison 1988; Brandt et al. 1994). The reproductive period for the two present gnathiid species is well under way in July for *C. robusta* and in September for *C. abyssorum* and is not showing any sign of decrease in October for either of the two species. A quick disintegration of dead males could explain the low number of males of digestive caeca stage III and of dead males in the samples. The data demonstrate a tendency towards settling of pranizae and moulting into adults in all sampling months. Thus, the present results indicate continuous reproduction probably lasting most or all of the year for *C. robusta*, while it is not possible to suggest anything about the length of the reproductive period for *C. abyssorum* as only data for a limited period exist at the moment. Whether a seasonal component in the reproductive intensity exists introduced by the accessibility of fish hosts cannot be decided for the moment. Both gnathiid species appear very flexible regarding the cavities used by the reproducing adults as well as by the pranizae during the resting and digesting phases (present investigation and Klitgaard 1991; Jensen & Frederiksen 1992). In addition the cavities used are situated in species of sponges and stone corals commonly occurring in the investigated areas and having prolonged lifespans. A seasonality is therefore not expected to be introduced by the accessibility of suitable cavities.

The lifespans of *C. robusta* and *C. abyssorum* cannot be determined from the present material; living at low temperatures the adult males of both species are probably able to survive for long periods, probably several years on the caecal food reserves as reported for *C. calva* (Wägele 1988). In contrast to "harem" forming gnathiid species the males of *C. robusta* and *C. abyssorum* live mainly in monogamous relationships, each male probably surviving long enough to complete two or more consecutive female reproductive sequences. The females of both gnathiid species produce bigger and, in *C. abyssorum*, fewer pranizae compared to "harem" forming gnathiid species.

Thus, the present data show that a quite different strategy, as compared to earlier reports of biology and life history of adult gnathiids, is demonstrated by the two examined bathyal species of gnathiids in the cold Arctic Intermediate Waters of the North Atlantic. To demonstrate the existence of continuous reproduction and of seasonality in the reproductive intensity in *C. robusta* and *C. abyssorum* the best procedure would be to collect samples in the winter and spring months. This would, however, be difficult owing to the weather and ice conditions in these areas. An alternative solution might be to keep living animals in temperature controlled aquaria through whole lifespans of both species. As the hosts of the pranizae are not known this would first demand some experiments with different species of fish to find suitable hosts.

It would be of interest to compare the present results with the average number and size of embryos produced per female of *C. abyssorum* at the Faroe Islands, the females there being of an inferior size (Table 10) and living in small "harems" (Klitgaard 1991; Jensen & Frederiksen 1992). This is not possible at present as only one female of *C. abyssorum* carrying embryos and a minor number of ovigerous females were found in the sponges from the Faroe Islands, and unfortunately these had been squeezed during sampling being partly empty.

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Tables

Table 1. Systematic position of the seven examined sponge species (following Hartman 1982), number of examined specimens of each species and size range for examined specimens. Variation of the diameter of the excurrent openings in *Geodia mesotriaena* is also shown. (*) = *Hexadella dedritifera* was present in the samples as fragments from the sediment surface on seven GF stations, as episponge on *Isops phlegraei* on further seven GF stations and one BIOICE station and both as fragments and as episponge on *I. phlegraei* on two GF stations. (**) = *Caecognathia robusta* was accidentally found in a fragment of *Pseudosuberites hyalinus*. No further material of this species was however examined. As the find nevertheless indicates the association of *C. robusta* with this sponge species the record is included. (-) = no measurements were made.

Order	Family	Species	No. of specimens examined	Diameter (cm)	Height (cm)	Diameter Excurrent openings (cm)
Astrophorida	Geodiidae	*Geodia mesotriaena* (Hentschel, 1929)	713	1.0-14.1	1.0-10.5	0.01-2.11
-	Theneidae	*Thenea valdiviae* Lendenfeld, 1906	389	1.5-10.0	-	-
-	-	*T. levis* Lendenfeld, 1906	91	2.0-15.0	-	-
-	-	*T. abyssorum* Koltun, 1959	147	0.5- 4.0	-	-
-	-	*T. muricata* (Bowerbank, 1858)	16	3.5-20.5	-	-
Dendroceratida	Aplysillidae	*Hexadella dedritifera* Topsent, 1913	*	-	-	-
Hadromerida	Suberitidae	*Pseudosuberites hyalinus* (Ridley & Dendy, 1887)	**	-	-	-

Table 2. Previous records of *Caecognathia robusta* and *C. abyssorum*. Numbers in parenthesis refer to source of information: Sars 1871 (1), 1879 (2), 1885 (3), 1899 (4); Hansen 1895 (5), 1916 (6); Stebbing 1913 (7); Stephensen 1912 (8), 1913 (9), 1937 (10), 1943 (11); Monod 1926 (12); Hentschel 1929 (13); Gurjanova 1933 (14), 1964 (15); Gorbunov 1946 (16); Anon. 1978 (17); Klitgaard 1991 (18); Barthel & Brandt 1995 (19); E. Willassen pers. commn (20). BIOFAR station data in Nørrevang et al. (1994). (-) = missing record. (*) = the specimen(s) were found in a sponge. (?) = the sex and stage of the specimens are not reported. (¤) = see text for explanation.

Geographical area	Expedition	Date	Depth (m)	Temp. (°C)	*Caecognathia robusta*	*Caecognathia abyssorum*
West of Ireland	The Porcupine Expedition St.no. 13; (6), (7)	18.05. 1869	381	9.8		1♂
Norway	Hjelte Fiord, SW of Færoy, St. no. 7; (12), (20)	1892	90-130	-		1♂*, 1 juv
Norway	Hardanger Fiord, at Utne; (1), (4), (12)	1871	376	-		1♀
Norway	Trondheim Fiord; (12)	-	-	-		1 juv.
Norway	Haswik, West Finmark; (4), (12)	-	282-376	-		3♂, 1♀
Between Finmark and Bjørnøya	The Norwegian North-Atlantic Exp. St. no. 290; (2), (3), (6), (12)	07.07. 1878	349	3.5	3 juv.	
Between Finmark and Bjørnøya	Prince of Monaco St.no. 960; (6), (12)	29.07. 1898	393	-	1♂	
West of Svalbard	The Norwegian North-Atlantic Exp. St.no. 359; (2), (3), (6), (8), (9), (12)	12.08. 1878	761	0.8	10♂	
North of Svalbard	Römer & Schaudin St.no. 41 (13)	11.08. 1898	1000	-	1-2♂*¤	
The Barents Sea	- ; (14)	-	-	-	1?	
The Arctic Sea	The G. Sedov Exp. St.no. 32; (15), (16)	26.08. 1935	360	-	?	
The Arctic Sea	The G. Sedov Exp. St.no. 55; (15), (16)	09.09. 1935	300	-	?	
The Faroe Islands	BIOFAR St.no. 043; (18)	19.07. 1987	235	7.2		5 juv.*
The Faroe Islands	BIOFAR St.no. 052; (18)	19.07. 1987	235	7.1		2 juv.*
The Faroe Islands	BIOFAR St.no. 148; (18)	07.05. 1988	234	7.2		(1♂, 3 juv.)*
The Faroe Islands	BIOFAR St.no. 150; (18)	07.05. 1988	157	8.1		20 juv.*
The Faroe Islands	BIOFAR St.no. 156; (18)	07.05. 1988	243	7.0		15 juv.*
The Faroe Islands	BIOFAR St.no. 191; (18)	10.05. 1988	170	7.7		1 juv.*
The Faroe Islands	BIOFAR St.no. 205; (18)	11.05. 1988	160	8.1		(2♂, 21 juv.)*
The Faroe Islands	BIOFAR St.no. 282; (18)	15.07. 1988	253	7.0		3 juv.*
The Faroe Islands	BIOFAR St.no. 346; (18)	22.07. 1988	338	6.4		20 juv.*
The Faroe Islands	BIOFAR St.no. 375; (18)	02.11. 1988	245	7.1		(6♂, 17 juv.)*
The Faroe Islands	BIOFAR St.no. 451; (18)	03.06. 1989	398	5.0		(11♂, 2♀, 27 juv.)*
The Faroe Islands	BIOFAR St.no. 453; (18)	03.06. 1989	400	6.2		(3♂, 3♀, 12 juv.)*
The Faroe Islands	BIOFAR St.no. 468; (18)	05.06. 1989	281	7.3		2 juv.*
The Faroe Islands	BIOFAR St.no. 469; (18)	05.06. 1989	381	5.5		(11♂, 7♀, 46 juv.)*
The Faroe Islands	BIOFAR St.no. 471; (18)	05.06. 1989	293	7.2		(2♂, 6 juv.)*
The Faroe Islands	BIOFAR St.no. 474; (18)	21.07. 1989	246	7.1		22 juv.*
The Faroe Islands	BIOFAR St.no. 476; (18)	21.07. 1989	252	7.0		6 juv.*
The Faroe Islands	BIOFAR St.no. 483; (18)	22.07. 1989	405	4.0		3 juv.*
The Faroe Islands	BIOFAR St.no. 540; (18)	31.07. 1989	480	5.6		(1♂, 2 juv.)*
The Faroe Islands	BIOFAR St.no. 558; (18)	30.11. 1989	252	7.9		1 juv.*
The Faroe Islands	BIOFAR St.no. 559; (18)	30.11. 1989	254	7.9		(2♂, 1 juv.)*
East of Iceland	The Thor Expedition; (6), (10), (12)	16.07. 1902	130	-		1♂
South of Iceland	The Danish Ingolf Expedition St.no. 55; (6), (12)	19.05. 1896	595	5.9		1♂
Southwest of Iceland	The Danish Ingolf Expedition St.no. 81; (6), (12)	14.06. 1896	913	6.1		2♂*, 1 juv.
West of Iceland	The Danish Ingolf Expedition St.no. 9; (6), (11), (12)	20.05. 1895	555	5.8	1♂	1♂
North of Iceland	BIOICE St.no. 2758; (19)	01.08. 1995	786	-0.4	1♂*	
North of Iceland	BIOICE St.no. 2769; (19)	02.08. 1995	519	-0.4	(1♂, 5♀, 4?)*	
Near Jan Mayen	The Ryder Expedition; (5), (6), (8), (9), (12)	27.06. 1891	884	-	1♂	
Off East Greenland	The Ryder Expedition; (5), (6), (8), (9), (11), (12)	17.08. 1892	314	-	1♂, 1♀, 1 juv.	
East Greenland, Scoresbysund area, Rathbone Island	II Amdrup Expedition; (6), (11), (12)	-	175 or 300	-		1♂*
Northeast Greenland	ARK X/1 St.no. 31-16; (19)	21.07. 1994	800	-	(14♂, 7♀, 6 juv.)*	
Northeast Greenland	ARK X/1 St.no. 31-20; (19)	23.07. 1994	840	-	(7♂, 6♀, 2 juv.)*	
Northeast Greenland	ARK X/1 St.no. 31-25; (19)	27.07. 1994	777	-	(5♂, 1♀, 4 juv.)*	
The Davis Strait, St. Hellefiske Banke	The Greenland Fisheries Investigations; (17)	25.08. 1976	176	-		6♂, 2♀, 2 juv.
The Baffin Bay	The Swedish Expedition; (6), (12)	1871	208	-	1♂	
-	The Danish Ingolf Expedition St.no. unknown; (6)	1895-1896	-	-	(1♂, 2♀, 1juv.)*	

Table 3. Stations and sponge species in which *Caecognathia robusta* (*C.r.*), *C. abyssorum* (*C.a.*) and *C. hirsuta* (G. O. Sars, 1877) (*C.h.*) as well as gnathiid pranizae (*C.*sp.) were found. *G.m.* = *Geodia mesotriaena*, *H.d.* = *Hexadella dedritifera*, *T.v.* = *Thenea valdiviae*, *T.m.* = *T. muricata* and *P.h.* = *Pseudosuberites hyalinus*. (?) = the gnathiid was found loose in the sample without substratum. (-) = missing record. Sal. = salinity. RP = Rothlisberg & Pearcy epibenthic sledge, Td = triangular dredge, Ds = detritus sledge, Bt = bottom trawl and Rd = rock dredge.

St. nr.	Date	Position		Depth	Temp.	Sal.	Gear	Gnathiidae			
		N	W	(m)	°C			*C.r.*	*C.a.*	*C.h.*	*C.*sp.
BIOICE 2010	20-07-1991	65°30.22'	11°23.45'	619	-0.40	-	RP				*T.v.*
BIOICE 2022	22-07-1991	66°36.69'	12°43.32'	325	-	-	Td	*G.m.*; *T.v.*			*T.v.*
BIOICE 2023	22-07-1991	66°33.23'	13°15.26'	294	1.40	-	Ds	*G.m.*			
BIOICE 2032	23-07-1991	66°54.75'	13°28.26'	564	-0.50	-	Ds	*T.v.*			
BIOICE 2033	23-07-1991	66°54.81'	13°30.65'	552	-0.50	-	RP	*T.v.*			*T.v.*
BIOICE 2089	05-07-1992	67°13.08'	17°50.34'	517	-0.40	34.90	Ds				*T.v.*
BIOICE 2093	05-07-1992	67°11.85'	17°45.30'	407	-0.30	34.90	Ds	*T.v.*			*T.v.*
BIOICE 2424	03-07-1993	63°10.27'	20°09.54'	495	6.50	35.08	RP				*T.m.*
BIOICE 2501	12-07-1993	66°25.24'	25°50.32'	630	-0.40	34.87	Ds			*H.d.*	*H.d.*
BIOICE 2518	13-07-1993	66°36.94'	25°33.59'	749	-0.50	34.87	Ds	*G.m.*			
GF 87SM0038	22-10-1987	66°35'	30°46'	490	0.69	34.74	Bt	*G.m.*			
GF 92PA0160005	11-10-1992	67°06.9'	27°03.8'	371	0.72	34.75	Bt	*G.m.*			
GF 92PA0160011	12-10-1992	66°11.9'	28°37.5'	339	1.14	34.79	Bt		*H.d.*		*H.d.*
GF 92PA0160013	13-10-1992	66°00.2'	29°11.8'	307	0.88	34.85	Bt		*H.d.*		
GF 92PA0160014	13-10-1992	66°08.9'	29°10.0'	306	1.24	34.80	Bt		*H.d.*		*H.d.*
GF 92PA0160028	15-10-1992	66°44.2'	28°16.5'	314	0.71	34.80	Bt		*H.d.*		*H.d.*
GF 92PA0160042	18-10-1992	66°46.3'	29°51.9'	322	0.82	34.77	Bt		*H.d.*		
GF 92PA0160048	19-10-1992	67°19.3'	31°32.2'	582	0.84	34.85	Bt	*P.h.*			
GF 92PA0160052	20-10-1992	66°07.5'	32°36.7'	294	1.73	34.74	Bt		*H.d.*		*H.d.*
GF 92PA0160055	22-10-1992	66°27.1'	31°39.4'	337	1.68	34.72	Bt		*H.d.*		*H.d.*
GF 94PA0090001	17-09-1994	67°24.7'	26°38.1'	306	0.33	34.70	Bt	*G.m.*			
GF 94PA0090002	17-09-1994	67°37.4'	27°50.3'	274	0.78	34.65	Bt	*G.m.*			*H.d.*
GF 94PA0090009	19-09-1994	67°13.6'	30°32.9'	441	0.93	34.76	Bt	*G.m.*; *H.d.*	*H.d.*		*H.d.*
GF 94PA0090010	19-09-1994	67°19.1'	30°29.1'	241	-	-	Bt				*H.d.*
GF 94PA0090019	21-09-1994	65°43.1'	34°23.7'	360	2.38	34.70	Bt	*H.d.*	*H.d.*		*H.d.*
GF 94PA0090020	22-09-1994	66°02.0'	32°46.4'	282	2.07	34.73	Bt	*H.d.*	*H.d.*	*H.d.*	*H.d.*
GF 94PA0090026	24-09-1994	66°21.5'	32°46.4'	467	0.52	34.80	Bt	*G.m.*; *H.d.*	*H.d.*		*H.d.*
GF 94PA0090041	28-09-1994	67°07.1'	28°26.5'	335	0.27	34.76	Bt	*G.m.*			
GF 94PA0090043	28-09-1994	66°54.3'	27°44.8'	372	0.17	34.76	Bt	*G.m.*			
GF 94PA0090045	29-09-1994	66°40.8'	27°00.7'	454	-0.04	34.85	Bt	*G.m.*			
GF 94PA0090046	29-09-1994	66°40.4'	27°24.0'	374	0.04	34.84	Bt	*G.m.*	*H.d.*		*H.d.*
GF 94PA0090049	30-09-1994	66°08.4'	27°55.4'	471	0.21	34.84	Bt				*H.d.*
GF 94PA0090062	03-10-1994	67°09.1'	30°32.3'	467	0.63	34.80	Bt	*G.m.*; *H.d.*	*H.d.*		*H.d.*
GF 94PA0090069	04-10-1994	66°54.1'	28°54.4'	309	0.40	34.79	Bt	*G.m.*			
Ingolf St.no. 90	24-06-1896	64°45'	29°06'	1070	4.40	-	-	*G.m.*			
Lynch St.no. 9	06-10-1972	67°58.5'	18°23.6'	-	-	-	Rd	*G.m.*			
Polarstern 223	05-08-1990	81°48'	10°28'	550	-	-	Bt	*G.m.*			
BIOFAR 041	19-07-1987	61°13.3'	04°46.5'	780	-0.60	-	RP	?			

Table 4. Occurrence of *Caecognathia robusta* in *Geodia mesotriaena* collected respectively during the BIOICE programme 1991-94, by the Greenland Institute for Natural Resources in the Denmark Strait (GF stations), during the Danish Ingolf Expedition 1895-96, the Lynch Expedition 1972 and during R/V *Polarstern* cruise ARK VII/2 in 1990 at NE-Greenland. The BIOICE stations have been divided in samples taken north of Iceland and in the Denmark Strait respectively. (-) = not possible to estimate.

Expedition	No. of sponges examined	No. of sponges with *Caecognahtia robusta*	% occurrence of *Caecognathia robusta* in the sponges
BIOICE, North Iceland	13	7	53.8
BIOICE, Denmark Strait	47	2	4.3
GF stations	579	107	18.5
The Ingolf Exp.	66	1	(1.5)
The Lynch Exp.	5	2	-
R/V *Polarstern* cruise	3	1	-
Total number of sponges	713	120	16.8

Table 5. Number of preoscular cavities of *Geodia mesotriaena* of each station inhabited by *Caecognathia robusta*, and the distribution of *C. robusta* males and females in these cavities. († ♂) = dead remains of a male.

St.no.	No. of inhabited cavities	1♂	1♂ + 1♀	1♂ + 2♀	1♂ + 3♀	1♀	1 Praniza	†♂
BIOICE 2022	7		2	2	2		1	
BIOICE 2023	1		1					
BIOICE 2518	2	1	1					
GF 87SM0038	1						1	
GF 92PA0160005	1		1					
GF 94PA0090001	12	11	1					
GF 94PA0090002	80	30	32	5	1	6	4	2
GF 94PA0090009	2	2						
GF 94PA0090026	1		1					
GF 94PA0090041	3		3					
GF 94PA0090043	4		2			1	1	
GF 94PA0090045	1	1						
GF 94PA0090046	1	1						
GF 94PA0090062	1	1						
GF 94PA0090069	1			1				
Ingolf Exp. St.no. 90	1			1				
Lynch Exp. St.no. 9	2		2					
Polarstern St.no. 223	1	1						
Total No.	122	48	46	9	3	7	7	2
%	100	39.3	37.7	7.4	2.5	5.7	5.7	1.6

Table 6. Number of single males, females and pairs of *Caecognathia abyssorum* and *C. robusta* as well as of single pranizae (*C.* sp.) and single males of *C. hirsuta* found in *Hexadella dedritifera* growing on the sediment surface. († ♂) = dead remains of a male.

St.no.	*Caecognathia abyssorum*			*Caecognathia robusta*				*C.* sp.	*C. hirsuta*
	1♂	†♂	1♂ + 1♀	1♂	†♂	1♂ + 1♀	1♀	pranizae	1♂
GF 92PA0160055	1							13	
GF 94PA0090009			1			2	1	14	
GF 94PA0090010								2	
GF 94PA0090019	3		2	12		4		14	
GF 94PA0090020	4	2	2	4	4	4		25	1
GF 94PA0090026	2		5			2		81	
GF 94PA0090046	6	1	5					17	
GF 94PA0090049								16	
GF 94PA0090062	1			7		4		23	
Total number	17	3	15	23	4	16	1	205	1

Table 7. Number of single males, females and pairs of *Caecognathia abyssorum* and *C. robusta* as well as of single pranizae (*C.* sp.) and single males of *C. hirsuta* found in *Hexadella dedritifera* growing as episponge on *Isops phlegraei*. The number of specimens of *I. phlegraei* on which the gnathiids were found are shown. († ♂) = dead remains of a male.

St.no.	No. of specimens of *Isops phlegraei*	*Caecognathia abyssorum*				*C. robusta*	*C.* sp.	*C. hirsuta*
		1♂	†♂	1♂ + 1♀	1♀	1♂	pranizae	1♂
GF 92PA0160011	1	4					1	
GF 92PA0160013	2			3	3			
GF 92PA0160014	2	1					2	
GF 92PA0160028	2	2	2				1	
GF 92PA0160042	1	1						
GF 92PA0160052	1	4	1	6			2	
GF 94PA0090002	1						1	
GF 94PA0090026	11	10	1	11	1	1	14	
GF 94PA0090062	2					1	2	
BIOICE 2501	2						1	1
Total number	25	22	4	20	4	2	24	1

Table 8. Stations and number of specimens of *Thenea valdiviae* (*T. v.*), *T. muricata* (*T. m.*) and *Pseudosuberites hyalinus* (*P. h.*) on which gnathiids were found and the distribution of these in the sponges. († ♂) = dead remains of a male.

St. no.	Sponge species	No. of specimens	*Caecognathia robusta* 1♂	†♂	1♂ + 1♀	Swollen Pranizae	Segmented Pranizae
BIOICE 2010	*T. v.*	1				1	
BIOICE 2022	*T. v.*	2			1		1
BIOICE 2032	*T. v.*	1	1				
BIOICE 2033	*T. v.*	2	1			1	
BIOICE 2089	*T. v.*	1				1	
BIOICE 2093	*T .v.*	1			1		2
BIOICE 2424	*T. m.*	1				1	
GF 92PA0160048	*P. h.*	1	1	1			

Table 9. Size range (Min. – Max. length) and average length (±SD) of adult males, females and swollen pranizae of third stage of *Caecognathia robusta* shown for the different expeditions and sponge species. (n) = number of ♂/♀/Praniza measured. *G.m.* = *Geodia mesotriaena*, *T.v.* = *Thenea valdiviae*, *H.d.* = *Hexadella dedritifera*, *P.h.* = *Pseudosuberites hyalinus*. (-) = no values.

Expedition	Sponge species	n ♂	Min. – Max. length ♂ (mm)	Average length ♂ (mm)	n ♀	Min. – Max. length ♀ (mm)	Average length ♀ (mm)	n Praniza	Min. – Max. length Praniza (mm)	Average length Praniza (mm)
BIOICE	*G.m.*	9	6.6-7.5	7.1±0.29	7	5.3-6.4	5.9±0.34	7	5.3-7.4	6.6±0.69
BIOICE	*T.v.*	4	5.1-6.1	5.7±0.45	2	5.7-6.3	6.0±0.42	-	-	-
GF	*G.m.*	73	4.8-7.9	6.4±0.68	35	4.3-7.1	5.7±0.85	16	5.5-7.5	6.5±0.80
GF	*H.d.*	34	4.1-6.3	5.4±0.55	11	4.7-6.0	5.3±0.48	3	5.2-6.4	5.8±0.60
GF	*P.h.*	1	6.4		-	-	-	-	-	-
Ingolf Exp.	*G.m.*	1	8.1		1	6.4		1	8.3	
Lynch Exp.	*G.m.*	1	7.2		2	5.0-7.1	6.1±1.48	-	-	-
R/V *Polarstern*	*G.m.*	1	7.5		-	-	-	-	-	-
BIOFAR	-	1	5.1		-	-	-	-	-	-
Total		125	4.1-8.1	6.1±0.83	58	4.3-7.1	5.7±0.76	27	5.2-8.3	6.5±0.84

Table 10. Size range (Min. – Max. length) and average length (±SD) of adult males, females and swollen pranizae of third stage of *Caecognathia abyssorum* shown for the present GF material from the Denmark Strait and for comparison for the BIOFAR collection (Klitgaard 1991) from the Faroe Islands. (n) = number of ♂/♀/Praniza measured. *H.d.* = *Hexadella dedritifera*, *S.p.* = *Stryphnus ponderosus*, *S.n.* = *Stelletta normani*, *T.i.* = *Tragosia infundibuliformis*, *P.r.* = *Phakellia robusta* and *A.a.* = *Axinella arctica*. (-) = no values.

Expedition	Sponge species	n ♂	Min. – Max. length ♂ (mm)	Average length ♂ (mm)	n ♀	Min. – Max. length ♀ (mm)	Average length ♀ (mm)	n Praniza	Min. – Max. length Praniza (mm)	Average length Praniza (mm)
GF	*H. d.*	67	2.9-4.0	3.4±0.28	24	3.1-4.2	3.6±0.27	12	3.6-4.9	4.3±0.47
BIOFAR	*S.p.* + *S.n.* + *T.i.* + *P.r.* + *A.a.*	31	1.9-2.5	2.1±0.18	10	2.0-2.5	2.3±0.19	-	-	-

Table 11. The number of flagellar articles of antenna 2 of respectively 10 segmented and 10 swollen pranizae found singly in *Hexadella dedritifera*, and of some adult males and females and third stage pranizae of *Caecognathia robusta* and *C. abyssorum*. For comparison the number of flagellar articles were also counted for some adult males and females as well as pranizae of *C. abyssorum* collected at the Faroe Islands (Klitgaard 1991).

No. of flagellar articles of antenna 2	Single Pranizae – *Hexadella dedritifera*		*Caecognathia robusta*			*Caecognathia abyssorum* The Denmark Strait			*Caecognathia abyssorum* The Faroe Islands		
	Segmented	Swollen	♂	♀	Praniza	♂	♀	Praniza	♂	♀	Praniza
6							2	1	5	5	20
7	10	10	5	5	10	5	4	9			

Table 12. Total number of embryos per female of *Caecognathia robusta* and *C. abyssorum*, number of embryos measured (only intact embryos were measured) and the average length (±SD) of these. The females are arranged according to increasing size. (*) = some embryos had slipped through the marsupial valves and the female was partly empty, the number is therefore not representative for this female. (+) = the female contained embryos but it was not possible to count these. (?) = the embryos could not be measured. ("Average") = average number of embryos per female ±SD.

	Caecognathia robusta				*Caecognathia abyssorum*			
♀ no.	Length of ♀ (mm)	No of embryos per ♀	No. of embryos measured	Average length of embryos (mm)	Length of ♀ (mm)	No. of embryos per ♀	No of embryos measured	Average length of embryos (mm)
1	5.5	18*	18	2.07±0.09	3.5	16	11	1.20±0.08
2	5.8	59	58	1.57±0.17	3.5	24	21	1.15±0.05
3	5.9	72	70	1.53±0.17	3.5	54	52	1.10±0.07
4	5.9	+		?	3.6	22	20	1.61±0.08
5	6.0	105	104	2.05±0.08	3.6	30	22	1.19±0.06
6	6.7	110	105	1.72±0.18	3.8	25	15	1.20±0.08
7	6.7	139	139	2.03±0.07	3.9	58	58	1.22±0.06
8	7.1	175	173	2.24±0.07				
Average		110±42.7				33±16.5		

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