RESEARCH ARTICLE

Reproductive biology of deep-water calanoid copepods from the Arctic Ocean

K. N. Kosobokova · H.-J. Hirche · R. R. Hopcroft

Abstract Reproductive modes and egg production were studied in 15 species of meso- and bathypelagic copepods from nine Calanoida families in the Arctic Ocean. During shipboard incubation, females of seven species released eggs freely into the water and females of three species produced membrane-bound egg sacs. One species, *Aetideopsis rostrata*, produced a mass of eggs looking like an egg sac, but the "sac" lacked a membrane and disintegrated within 2 h. Females of four additional species were encountered with membrane-bound egg sacs in the preserved samples. In most families, only one reproductive mode, either egg-carrying (the Euchaetidae, Augaptilidae), or broadcast spawning (the Heterorhabdidae, Spinocalanidae, Scolecitrichidae, Tharybidae, Bathypontiidae) was observed. In contrast, different genera of the Aetideidae family demonstrated different reproductive modes, with broadcast spawning predominant in the benthopelagic species, and both broadcast spawning and egg-brooding in the planktonic species. Clutch size and egg diameter varied widely between species in both broadcast spawners and egg-brooders. In broadcast spawners, the clutch size varied from 1 to 95 eggs female^{-1}, while the average egg diameter ranged from 152 to 440 μm. The clutch size for egg brooders varied between 3 and 82, while average egg diameter varied from 258 to 732 μm. Deep-water broadcast spawners produced much larger eggs compared to surface-dwelling broadcast spawning species. This larger egg size may result in a reduction, or elimination, of feeding during naupliar stages, thereby improving the survival potential of deep-water species.

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Introduction and objectives

Knowledge on the reproductive biology, egg production and reproductive strategies of copepods has been derived primarily from the studies of small neritic species that are important as secondary producers in shelf seas (e.g. Sazhina 1971; Paffenhofer and Harris 1976; McLaren and Corkett 1981; Uye 1981; Jónasdóttir 1989; Kiørboe and Sabatini 1994; Hopcroft and Roff 1998; Halsband and Hirche 2001), and large grazers dominating the epipelagic zone of the open ocean (Conover 1967; Runge 1984; Hirche and Bohrer 1987; Hirche 1989, 1990; Smith 1990; Tourangeau and Runge 1991; Diel and Tande 1992; Kosobokova 1993, 1994; Ward and Shreeve 1995; Hirche and Niehoff 1996; Saito and Tsuda 2000; Kosobokova and Hirche 2001; Hirche and Kosobokova 2003; Hopcroft et al. 2005). Two basic reproductive modes are known for calanoid copepods: free-spawning (or broadcast spawning), where females release eggs freely into the water, and egg-brooding, where a female carries a

clutch of eggs attached to its genital somite until the nauplii hatch. Surprisingly, such basic knowledge of the life histories and reproduction of meso- and bathypelagic species remains very poor and scattered. Only a few deeper-dwelling species carrying resistant egg sacs (MacLellan and Shih 1974; Hopkins 1977, 1982; Ward and Robins 1987; Mauchline 1992, 1994, 1995; Ohman and Townsend 1998, Alonzo et al. 2000a, b; Auel 2004), and several free-spawning species (Matthews 1964; Yamaguchi and Ikeda 2000) have been studied.

Collection techniques for deeper-dwelling copepods are generally inappropriate for the assessment of their reproductive parameters (Ohman and Townsend 1998). The use of coarse meshes results in the loss of free eggs, and the long periods of time required to retrieve animals from the depth, together with abrasion in the nets, often causes females to be damaged, and their egg masses to be lost. Furthermore, in temperate and tropical regions animals are exposed to much higher surface temperatures after the long retrieval from great depths at low temperatures, making it almost impossible to collect live, unaffected females for egg production or rearing experiments. In contrast, polar regions, and the Arctic Ocean in particular, are characterized by only slight variations of temperature throughout the water column and are therefore suitable places for studies of egg production and reproductive biology of the deep-dwelling zooplankton species.

The midwater and deep-water copepod fauna of the Arctic Ocean consists of deep-water Atlantic, Pacific and bipolar species, plus species that are either widely distributed or endemic to the Arctic (Brodsky 1967; Dunbar and Harding 1968; Damkaer 1975; Kosobokova and Hirche 2000). Population stage structure in most deep-dwelling species indicates that they reproduce successfully in the Arctic Ocean (e.g. Harding 1966). Nonetheless, direct knowledge of their life cycles and reproductive biology is poor due to limited access to the ice-covered Arctic Ocean, the challenges involved in the collection and cultivation of live animals in the polar environment, and the low-numerical abundance of these species.

The present study aims to describe the eggs, and determine the reproductive investments, of midwater and deep-dwelling copepods of the Arctic Ocean. The major questions to be answered in the present study are: which reproductive modes exist in deep-water copepods in the Arctic? How do their egg and clutch size vary? What are the relationships between clutch, egg and female mass, and do these differ from relationships known for epipelagic species?

Methods

Reproductive biology and egg production of meso- and bathypelagic calanoid copepods were studied at total of 61 stations during four expeditions of R/V "Polarstern" in the Eurasian Basin of the Arctic Ocean and Fram Strait, plus one cruise of USCGC "Healy" in the Canada Basin (Fig. 1). Collections for live material were made with a bongo net (mesh size 310 and 500 μm) towed mostly from 500, 900 and 1,500 m to the surface (Table 1). Stratified samples were taken with a multinet (Hydrobios Kiel, mesh size 150 μm) between 0 and 3,000 m. All mature females were sorted immediately after capture. They were placed in 30 ml plastic beakers filled with pre-screened sea-water collected with water bottles from below 500 m. Single females were incubated at dim light at temperatures between –0.5 and +0.5°C. Incubation varied from 7 to 27 days. The females were checked every 12 h for egg production. Eggs of free-spawning species were counted and removed; subsequently, egg size was measured and egg morphology was studied under a stereo microscope. For egg-brooding species, the number of eggs was counted in the egg sacs after preservation in 4% hexamine buffered formaldehyde. The formaldehyde-preserved multinet catches obtained during the same cruises (for details of sampling see Kosobokova and Hirche 2000) were used to enumerate and measure eggs in the egg sacs of egg-brooding species. The clutch size was estimated as the number of eggs produced during one spawning event by a free-spawning or egg-brooding female. Egg production rate was estimated for females of only one species, *Scaphocalanus acrocephalus*. Each female's egg production rate was calculated as the mean over the incubation period (up to 27 days).

Female prosome and total length were measured under stereo microscope at 25× magnification. For dry mass (DM) measurements, single live females were sorted out of the samples at random. They were briefly dipped into distilled water and stored in pre-weighed tin caps at –28°C. In the laboratory, they were dried at 60°C for 24 h and weighed on a Sartorius microbalance. For some species, DM was taken from Mizdalski (1988), Auel (1999) and Auel and Hagen (2005). When DM data were not available, the female wet mass (biovolume) was calculated using nomogramms provided by Chislenko (1968), assuming female DM is 17% of wet mass and carbon is 45% of DM (Båmstedt 1986). The egg volume was calculated from the egg diameter, and egg carbon was assumed to be 0.14 pg μm^{-3} (Kiørboe and Sabatini 1995).

Fig. 1 The Arctic Ocean. Location of stations where females for egg production experiments and females with egg sacs were collected
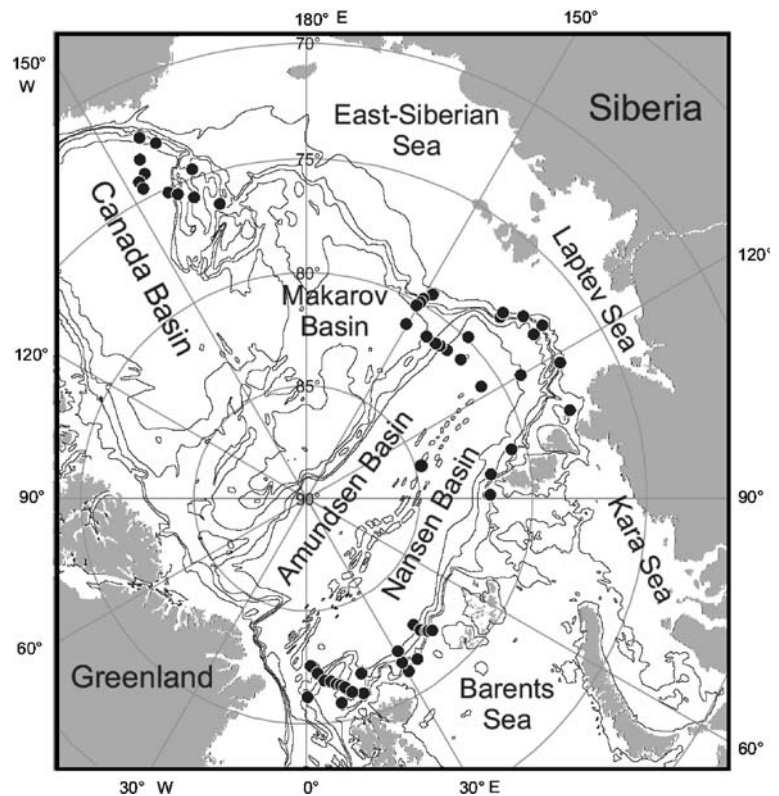
As the net hauls used for egg production studies were often collected over a wide depth range, we used the data from stratified multinet zooplankton collections from the same cruises to establish species specific depth ranges (Table 1). Calibrated images of living egg-carrying females and eggs were taken using an Insight 4 MegaPixel digital camera (Diagnostic Instruments, Sterling Heights, MI, USA) mounted on a Leica MZ16 dissecting microscope.

Results

In total, successful reproduction was observed in 172 specimens of 15 species of meso- and bathypelagic calanoid copepods from nine families. Of these, 11 species produced eggs under laboratory conditions (Tables 2, 3). Among them, *Chiridius obtusifrons* and *Aetideopsis minor* were also found with egg sacs in the field collections. The females of the other four species (Table 3) were collected together with their egg sacs.

Vertical distribution of target species

The vertical ranges of the species studied encompass the Arctic's three major water layers (Fig. 2). *Paraeuchaeta glacialis* was the only copepod which could be considered epi- to mesopelagic. However, females usually occur deeper than 50–100 m, below the epipelagic zone which is restricted to the upper 50 m in the Arctic Ocean (Vinogradov 1970; Kosobokova 1989). The vertical ranges of the other species suggest two major groupings (Fig. 2).

The first group consists of species with a wide vertical range, covering almost the entire water column from the surface to the bottom, but with their core of abundance at mesopelagic depths. Among them, *Chiridius obtusifrons* occurs from the surface throughout the Arctic and Atlantic water, but prefers the Arctic subsurface waters of 50–200 m (Fig. 2). *Scaphocalanus acrocephalus, Heterorhabdus norvegicus* and *Gaetanus tenuispinus* show a clear preference for the transition layer between the Arctic and Atlantic waters and the upper Atlantic water between 100 and 750 m. The less abundant copepods *Aetideopsis minor, Temorites brevis* and *G. brevispinus* can also be attributed to this group (Fig. 2).

The second group is represented by species that occupy Atlantic and Arctic Bottom water (Fig. 2). As many of them have higher abundance in Bottom water than Atlantic water, we considered them as predominantly bathypelagic in the Arctic Ocean. Absolute abundance of these species is low in comparison to the mesopelagic group.

Table 1 Station list and sampling protocol for egg production studies

Ship, cruise station number	Date	Latitude, N	Longitude	Sampling gear	Mesh size (μm)	Bottom depth (m)	Maximum depth of haul (m)	Number of stratified samples
"*Polarstern*"								
ARK IX/4								
6	12 August 1993	81°12′	30°36′E	MN	150	179	160	5
7	13 August 1993	81°40′	30°16′E	MN	150	494	490	5
14	13 August 1993	81°27′	34°35′E	MN	150	2,719	1,500	5
16	15 August 1993	82°12′	30°53′E	MN	150	2,465	1,500	5
19	18 August 1993	82°45′	40°15′E	MN	150	2,994	1,500	5
20	19 August 1993	82°23′	40°54′E	MN	150	1,990	1,500	5
24	20 August 1993	82°09′	42°02′E	MN	150	1,004	900	5
25	21 August 1993	82°07′	42°32′E	MN	150	546	500	5
27	21 August 1993	82°01′	43°34′E	MN	150	280	250	5
35	04 September 1993	78°23′	133°04′E	MN	150	2,062	2,000	5
38	05 September 1993	78°10′	133°25′E	MN	150	982	980	5
47	08 September 1993	77°11′	126°14′E	MN	150	990	990	5
50	10 September 1993	77°44′	125°46′E	MN	150	1,990	1,980	5
54	13 September 1993	79°11′	119°54′E	MN	150	3,071	3,067	5
62	17 September 1993	77°24′	118°11′E	MN	150	554	550	5
ARK XI/1								
7	26 July 1995	79°27′	148°07′E	MN	150	200	200	5
20	02 August 1995	77°42′	130°03′E	Bo	300, 500	490	460	–
31	11 August 1995	80°46′	103°23′E	MN	150	1,435	1,435	9
45	18 August 1995	80°00′	134°56′E	Bo	300, 500	3,200	1,500	–
47	20 August 1995	80°55′	132°00′E	Bo	300, 500	3,830	1,500	–
49	22 August 1995	81°03′	136°32′E	Bo	300, 500	2,700	500	–
51a	23 August 1995	81°07′	138°47′E	Bo	300, 500	1,750	1,500	–
52	24 August 1995	81°10′	140°06′E	MN	150	1,290	1,200	9
55	25 August 1995	81°11′	143°24′E	Bo	300, 500	1,690	1,500	–
57	27 August 1995	81°12′	150°15′E	Bo	300, 500	2,640	1,500	–
60	28 August 1995	80°17′	150°18′E	Bo	300, 500	1,500	1,500	–
62	29 August 1995	80°05′	149°51′E	Bo	300, 500	1,000	930	–
64	30 August 1995	70°53′	149°49′E	Bo	300, 500	500	400	–
65	30 August 1995	79°30′	148°14′E	MN	150	225	225	5
75	04 September 1995	80°56′	122°40′E	Bo	300, 500	3,580	1,500	–
83	07 September 1995	77°56′	113°33′E	MN	150	220	220	5
89	09 September 1995	82°21′	92°55′E	Bo	300, 500	2,656	2,000	–
91	10 September 1995	82°04′	91°02′E	MN	150	1,000	1,000	9
92	10 September 1995	82°02′	90°56′E	MN	150	525	525	5
93	10 September 1995	81°58′	91°01′E	MN	150	240	240	5
ARK XII								
48	05 August 1996	84°47′	105°47′E	MN	150	3,863	3,840	9
ARK XIII								
58	04 July 1997	81°06′	16°53′E	Bo	300, 500	998	900	–
59	05 July 1997	81°06′	16°18′E	Bo	300, 500	2,061	1,500	–
62	08 July 1997	80°55′	09°50′E	Bo	300, 500	1,015	950	–
67	14 July 1997	81°18′	00°22′E	Bo	300, 500	2,427	1,500	–
68	15 July 1997	81°24′	00°58′E	Bo	300, 500	2,925	1,500	–
79	20 July 1997	82°39′	01°25′E	Bo	300, 500	3,233	1,500	–
84	23 July 1997	82°19′	03°41′E	Bo	300, 500	2,179	1,500	–
87	26 July 1997	82°03′	05°18′E	Bo	300, 500	1,409	1,300	–
88	26 July 1997	81°58′	05°45′E	Bo	300, 500	928	900	–
89	27 July 1997	81°54′	07°44′E	Bo	300, 500	832	800	–
90	28 July 1997	81°45′	09°15′E	Bo	300, 500	844	800	–
91	29 July 1997	81°40′	10°26′E	Bo	300, 500	1,516	1,400	–
93	30 July 1997	81°17′	13°19′E	Bo	300, 500	2,250	1,500	–
"*Healy*"								
OE-05								
3	29 June 2005	72°24′	155°19′W	MN	150	1,759	1,715	9
4	02 July 2005	72°29′	155°08′W	MN	150	1,690	1,650	9
5	05 July 2005	73°24′	153°33′W	MN	150	3,850	3,000	9
6	08 July 2005	73°59′	153°40′W	MN	150	3,850	3,000	9

Table 1 continued

Ship, cruise station number	Date	Latitude, N	Longitude	Sampling gear	Mesh size (μm)	Bottom depth (m)	Maximum depth of haul (m)	Number of stratified samples
7	09 July 2005	74°18′	152°12′W	MN	150	3,841	3,000	9
8	10 July 2005	74°34′	152°11′W	MN	150	3,846	3,000	9
9	14 July 2005	75°10′	155°54′W	MN	150	3,854	3,000	9
10	15 July 2005	75°26′	157°01′W	MN	150	688	640	7
11	16 July 2005	75°54′	159°35′W	MN	150	1,615	1,570	9
13	20 July 2005	76°25′	163°29′W	MN	150	2,100	2,065	9
14	21–22 July 2005	74°41′	160°40′W	MN	150	798	710	7
15	24 July 2005	73°02′	156°59′W	MN	150	2,257	2,240	9

MN multinet, *Bo* bongo net

Table 2 Reproductive characteristics of meso- and bathypelagic broadcast-spawning copepods

Species	Female total length (mm)	Female prosome length (mm)	No observations	Range of clutch size, (eggs)	Clutch size, mean ± SD (eggs)	No observations	Range of egg diameter (μm)	Mean egg diameter ± SD (μm)	No observations
Family Aetideidae									
Gaetanus tenuispinus	3.7 ± 0.11	3.00 ± 0.13	19	6–17	11.7 ± 3.62	10	See Table 4		
Gaetanus brevispinus	4.4 ± 0.15		6	2–6	4.4 ± 1.52	5	See Table 4		
Aetideopsis rostrata	3.9 ± 0.18	3.00 ± 0.11	12	9–17	13.3 ± 4.04	3	270–300	282	4
Family Heterorhabdidae									
Heterorhabdus norvegicus	4.0 ± 0.22	2.8 ± 0.21	7	93–95	94	2	150–157	152.4 ± 2.76	6
Family Spinocalanidae									
Spinocalanus horridus	2.3 ± 0.12	1.7 ± 0.06	13	6–10	8.4 ± 1.67	5	210–246	222.4 ± 11.21	10
Family Scolecitrichidae									
Scaphocalanus acrocephalus	4.6 ± 0.15	3.53 ± 0.12	12	1–4	1.6 ± 0.65	130	310–403	363.4 ± 28.08	32
Family Tharybidae									
Tharybis groenlandica	1.2		1	2	–	1	163.8	163.8	2
Family Bathypontiidae									
Temorites brevis	2.0 ± 0.12	1.5 ± 0.04	10	2	–	1	No data	No data	–

All species spawned in laboratory

Egg laying and reproductive mode

Females of seven species (*Gaetanus tenuispinus*, *G. brevispinus*, *Spinocalanus horridus*, *Scaphocalanus acrocephalus*, *Heterorhabdus norvegicus*, *Temorites brevis* and *Tharybis groenlandica*) released eggs freely into the water in our incubations (broadcast spawners, Table 2). During egg-laying, they swam actively, extruding egg mass as a single or double stream. In most species, freshly laid eggs were usually pear-shaped or elongated with somewhat thinner "posterior" ends. Within several minutes after release, the eggs became sub-spherical and then rounded off. In all the species except for *Gaetanus tenuispinus* and *G. brevispinus*, only one membrane covering the egg mass was visible. The eggs of the latter two species possessed two membranes with a perivitelline space between them. This "double membrane" became visible within 1 h after egg deposition (Fig. 3). The inner membrane was close to the egg mass, the outer one was greatly

Table 3 Reproductive characteristics of meso- and bathypelagic egg-brooding copepods

Species	Female total length (mm)	Female prosome length (mm)	No observations	Range of clutch size, (eggs)	Clutch size, mean ± SD, (eggs)	No observations	Range of egg diameter (µm)	Mean egg diameter ± SD (µm)	No observations
Family Euchaetidae									
Paraeuchaeta glacialis[a]	9.73 ± 0.33	7.22 ± 0.22	20	54–82	71.7 ± 7.64	28	475–600	534.4 ± 34.76	20
Paraeuchaeta polaris[a]	7.28 ± 0.5	5.5 ± 0.06	6	5–6	5.8 ± 0.45	6	720–768	730.0 ± 16.05	17
Paraeuchaeta barbata[a]	10.9 ± 0.50	7.6 ± 0.38	20	10–20	14.25 ± 2.57	20	664–800	732.1 ± 28.57	60
Family Aetideidae									
Chiridius obtusifrons[b]	4.25 ± 0.27	3.04 ± 0.19	24	25–51	36.9 ± 5.57	18	273–325	290.4 ± 12.32	20
Aetideopsis minor[b]	3.2 ± 0.13	2.4 ± 0.09	6	7–12	9.5	4	252–270	257.6 ± 7.26	13
Family Augaptilidae									
Augaptilus glacialis[c]	4.6 ± 0.35	3.4 ± 0.22	8	3–4 (?)	4 (?)	1	430–444	435.3 ± 7.57	3
Euaugaptilus hyperboreus[a]	7.51 ± 0.1	5.05 ± 0.09	7	3–4 (?)	4 (?)	1	669–675	673.3 ± 3.79	3

[a] Collected with egg sacs

[b] Produced egg sacs in laboratory and collected with egg sacs

[c] Produced egg sacs in laboratory

swollen and produced an irregular bulbous exterior (Fig. 3a, b, d). During the course of development, the width of perivitelline space gradually increased, resulting in a considerable enlargement of the outer diameter and volume of the egg. In *G. tenuispinus*, a 36% increase of the diameter of the outer membrane was observed after 48 h (Table 4).

Fig. 2 Generalized vertical distribution patterns of 15 deep-water copepod species in the Arctic Ocean

Females of the other seven species (*Augaptilus glacialis*, *Euaugaptilus hyperboreus*, *Aetideopsis minor*, *Chiridius obtusifrons*, *Paraeuchaeta glacialis*, *P. polaris* and *P. barbata*) produced egg sacs in the laboratory or were found with egg sacs in net samples (egg-brooding spawners, Table 3). The most spectacular observations were that on egg-brooding of the deep-water augaptilids, *Augaptilus glacialis*, which produced an egg sac with only three eggs (Fig. 4a–c), and *Euaugaptilus hyperboreus*, where a female was found in a deep net sample carrying an egg sac with also three eggs (Fig. 4d). In both species the eggs were very large compared to female size. The anterior portion of the egg sac was elongated and empty, thus the eggs were hanging under the furcal rami hardly reachable by the swimming legs. The egg-brooding mode was additionally confirmed in the latter species by the presence of remains of the egg sac membrane attached to the genital segments of several other females (Fig. 4e).

Females of the three euchaetids, *Paraeuchaeta glacialis*, *P. polaris* and *P. barbata* were also egg-brooding. We did not observe their egg laying in the laboratory, but regularly found their females with egg sacs in the live and preserved samples (Fig. 5). All three species had resistant sacs covered with a strong, highly visible membrane (Fig. 5c, f). The colour of eggs was orange
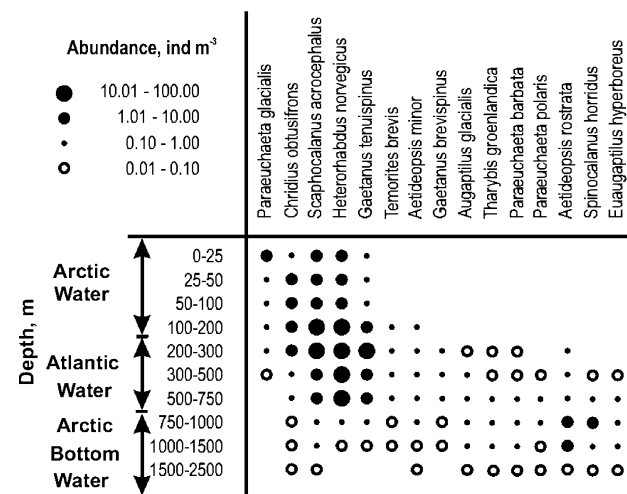
Fig. 3 Eggs of broadcast spawning copepods, *Gaetanus tenuispinus* (**a–b**) and *G. brevispinus* (**c**) with perivitelline space between inner and outer egg membranes
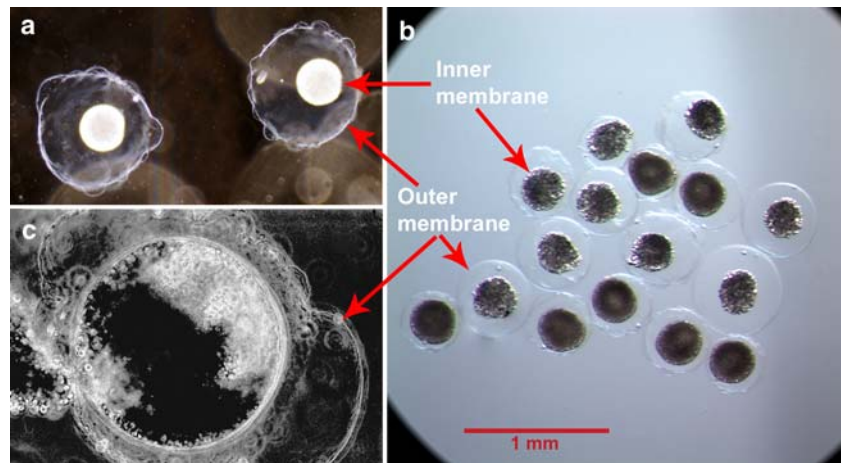

Table 4 Size of eggs in *Gaetanus tenuispinus* and *G. brevispinus* at different times after spawning

Species	No observations	Female total body length (mm)	Egg size (μm)			Time (h) after spawning
			No observations	Inner (mean ± SD)	Outer (mean ± SD)	
Gaetanus tenuispinus	17	3.8 ± 0.11	22	315.4 ± 9.73	531.4 ± 41.70	6
			8	317.8 ± 14.35	620.0 ± 115.99	24
			8	319.8 ± 3.08	723.0 ± 76.64	48
Gaetanus brevispinus	5	4.4 ± 0.15	6	440.0 ± 65.74	1,060 ± 111.50	4

to bright red in *P. barbata*, black to dark brown in *P. glacialis* and brown in *P. polaris*.

The females of aetideids *Chiridius obtusifrons* and *Aetideopsis minor* were found with egg sacs in the samples and also produced them in the laboratory. The orange-coloured eggs of *C. obtusifrons* were packed in a sac with a thick enclosing membrane (Fig. 6a). *A. minor* carried very fragile and adhesive egg sacs filled with light-orange eggs (Fig. 6b), but their sacs were easily torn off soon after egg laying. This explains why *A. minor* females were very rarely found with egg sacs in the net samples. A congener of *A. minor*, *Aetideopsis rostrata*, was once observed producing a mass of eggs looking like an egg sac. This "sac", however, lacked a membrane and disintegrated within 2 h, dispersing adhesive eggs. In all other cases, we missed the exact time of egg laying in *A. rostrata* and observed only dispersed eggs but no egg sacs.

Clutch size and egg size

Clutch and egg sizes showed a large variability (Tables 2, 3). In the broadcast spawners, clutch size varied from 1 to 95 eggs female^{-1} (Table 2). Very small clutches of one or two large eggs per spawning event (47 and 48.5% of all observed clutches, respectively) were observed in *Scaphocalanus acrocephalus*. Very seldom,

clutches of three or four smaller eggs were observed (2.3 and 2.3% of all clutches, respectively).

Small clutches of two eggs were also observed in *Temorites brevis* and *Tharybis groenlandica*. This, however, may not be representative, as only one observation is available for each species (Table 2). Females of the other broadcast spawners, *Gaetanus tenuispinus*, *G. brevispinus*, *Heterorhabdus norvegicus* and *Spinocalanus horridus*, produced larger clutches (Table 2).

The average egg diameter varied in the broadcast spawners from 152 to 440 μm (the maximum value corresponds to the inner diameter of the egg of *G. brevispinus*, Table 4). The smallest eggs were observed in *Heterorhabdus norvegicus*, which produced by far the largest clutches with up to 95 eggs (Table 2).

The number of eggs per clutch in egg-brooders varied between 3 and 82, while the average egg diameter ranged from 258 to 732 μm. The largest eggs and the lowest number of eggs per clutch were noted in the augaptilids *Augaptilus glacialis* and *Euaugaptilus hyperboreus*. It is noteworthy that four large, sausage-like oocytes were usually visible in the oviducts of mature females in both species. However, as we mentioned above, in the sacs of both egg-carrying *A. glacialis* and *E. hyperboreus* females only three eggs were present (Fig. 4a, b, d). More detailed examination under the microscope showed that there was one vacant pouch in the sac of each female,

Fig. 4 Egg-brooding Augaptilidae. **a**, **b** *Augaptilus glacialis* female with egg sac. **c** Egg of *A. glacialis* and the enclosing eggs sac membrane. **d** *Euaugaptilus hyperboreus* female with egg sac. **e** Remains of the egg sac membrane attached to genital segment of *E. hyperboreus* female
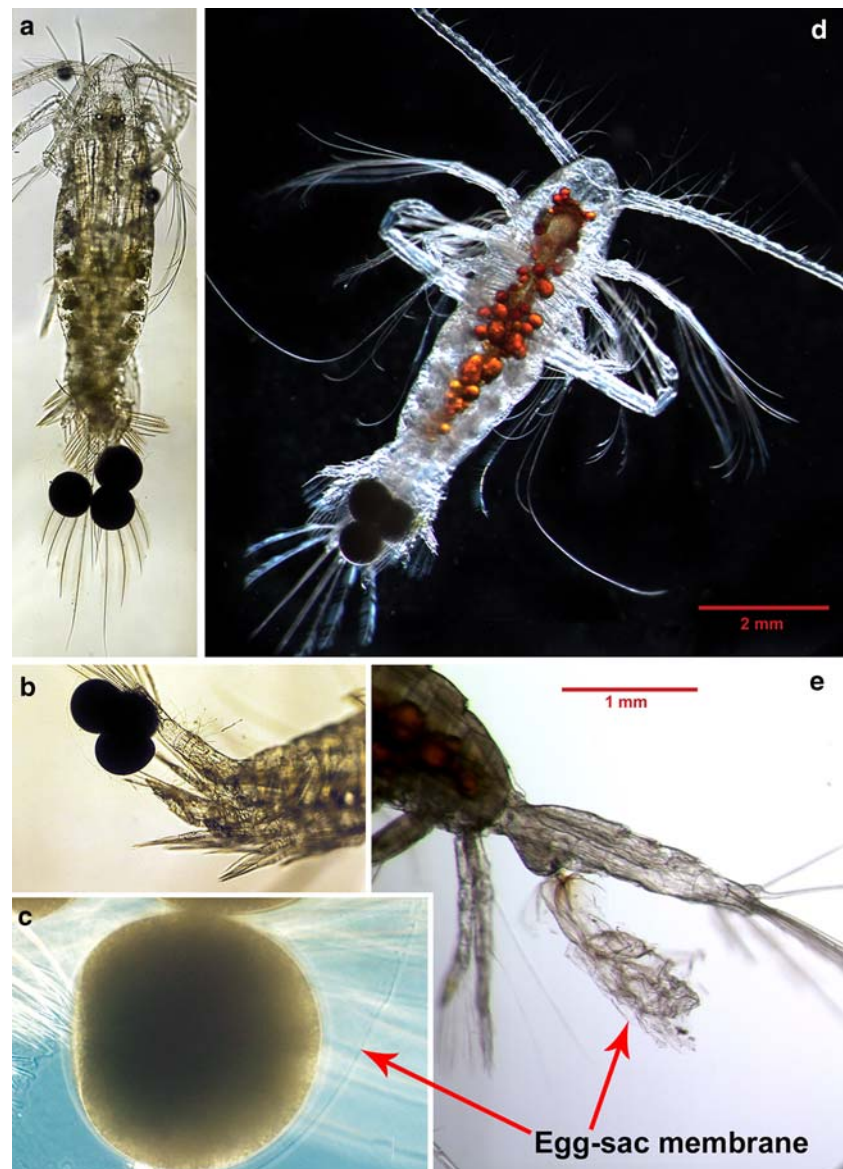
indicating prior presence of one additional egg. Thus, we assume the clutch size is four eggs in both species.

The egg production rates were obtained only for *Scaphocalanus acrocephalus* whose females released consecutive clutches at 1–4-day intervals (Table 5). In one female, eight consecutive clutches were obtained during 27 days with a total fecundity of 12 eggs female^{-1}. In other experiments, maximum number of eggs varied from 4 to 12 eggs female^{-1} during 8 and 27 days of incubation, respectively (Table 5). Average egg production rate varied from 0.19 ± 0.06 to 0.44 ± 0.26 egg female^{-1} days^{-1}, and specific egg production from 0.15 to 0.34% per day in different experiments (Table 5).

In all other species only one clutch was produced during the observation period of 1–3 weeks, and no information is available on their spawning intervals or egg production rates.

Brood size and reproductive investment

There was a broad range of reproductive investment among the species investigated, calculated as the proportion of female body carbon invested into a clutch (Table 6). In broadcast spawners this value varied from 1.6 to 20%. The lowest investment was observed in *Scaphocalanus acrocephalus*, which was the only species producing successive clutches almost daily (Table 5). The reproductive investment of egg brooders was somewhat higher than in broadcast spawners, and varied from 8.5 to 36.5% of female body mass (Table 6).

Fig. 5 Egg-brooding Euchaetidae: **a** *Paraeuchaeta glacialis* female with 40–50 eggs still in oviducts, inset illustrates relative size of egg-sac it will produce; **b** *P. glacialis* formalin-preserved egg sac; **c** *P. barbata* female; **d** *P. barbata* egg sac, life color; **e** *P. polaris* female; **f** *P. polaris* egg sac, life color
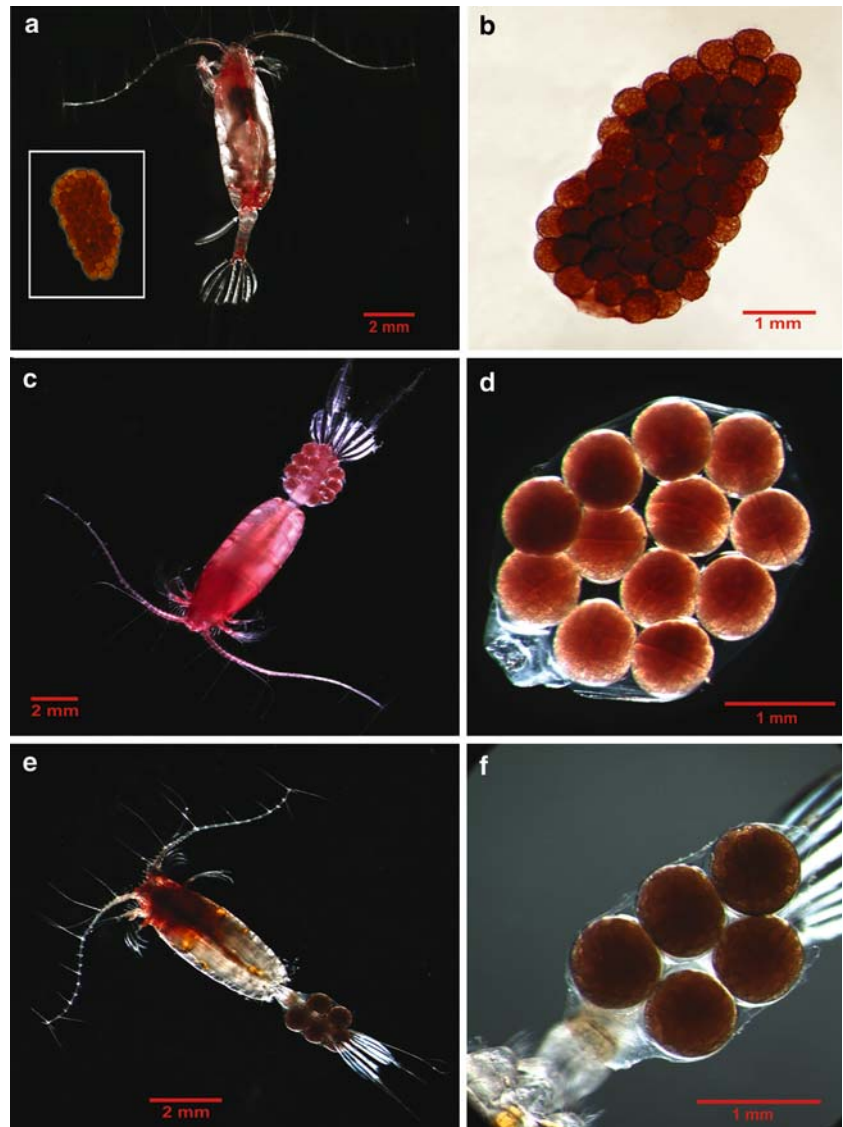
Fig. 6 Egg-brooding Aetideidae: **a** *Chiridius obtusifrons* females with sac; **b** *Aetideopsis minor* female with sac

Discussion

Reproductive modes

Both free-spawning and egg-brooding modes have been found in meso- and bathypelagic calanoids previously (e.g. Mauchline 1998; Yamaguchi and Ikeda 2000), but for many deep-dwelling species and Calanoida families such basic information is missing. For the families studied here, the reproductive modes have been known for the Euchaetidae (Hopkins 1977, 1982; Ward and Robins 1987; Mauchline 1992, 1994, 1995; Alonzo et al. 2000a, b; Auel 2004), a few Aetideidae (Matthews 1964; Mauchline 1998; Ohman and Townsend 1998; Yamaguchi and Ikeda 2000) and two species of Augaptilidae (Scott 1909; Mauchline 1998). For the other six Calanoida families (Tables 2, 3) they are described here for the first time.

Among the midwater and bathypelagic calanoids, reproduction has been most extensively studied in the Euchaetidae due to the robustness of their egg sacs. All of the euchaetid species studied so far are egg-brooders (Hopkins 1977, 1982; Ward and Robins 1987; Mauchline 1992, 1994, 1995, 1998; Auel 2004). For the three euchaetid species studied here, the eggs were also packed in an egg sac with a tough and highly visible enclosing membrane (Fig. 5).

Our observations on two species of the Augaptilidae (Fig. 4), together with earlier data on *Euaugaptilus similis* (=*Paraugaptilus similis* in Scott 1909) and *E. magnus* (Mauchline 1988; R. R. Hopcroft, personal observation), suggest this family is also brooding eggs. In both species studied here (Table 3), the eggs were

packed in a sac covered with a distinct membrane thinner than in euchaetids, but also very visible (Fig. 4b, c, e). The large egg size compared to the female size, and low number of eggs in a clutch (Table 3), were conspicuous features of these bathypelagic copepods.

Our observations and overview of published information on the reproductive modes of the Aetideidae show that different genera within this family use different reproductive modes (Table 7). It is noteworthy, that aetideids associated with the sea-floor use only the broadcast mode, while the planktonic species use both broadcast spawning and egg-brooding (Table 7).

In the benthopelagic species there is the ability to attach single eggs or the brood as a whole to floating objects or substrate (Matthews 1964), which is apparently an adaptation to the benthopelagic life style. Thus, the egg membrane in the benthopelagic *Aetideopsis armata* is adhesive, and the eggs stuck to any surface they came in contact with (Matthews 1964). In *Aetideus armatus*, the eggs were always found attached to fibrous material in the water, or to the sides of the vessel. The outer membrane was slightly convoluted and the appearance of the eggs suggested that during laying they were actively attached to some free floating surface (Matthews 1964). In *Bradyidius armatus* (=*B. bradyi* in Matthews 1964) the eggs were always found clustered into distinct groups attached to the substrate, in contrast to the wide scattering of *Aetideopsis armata* eggs.

The planktonic members of this family demonstrate a wide variety of ways of egg laying, from free-spawned eggs in *Gaetanus*, fragile adhesive egg sacs in *Aetideopsis minor*, to sacs covered with a robust membrane,

Table 5 Clutch size, spawning intervals, egg production rate (*EPR*) and specific egg production rate (*SEPR*) of *Scaphocalanus acrocephalus*

Cruise, station number	Date	Number of females, (individuals)	Incubation duration (days)	Clutch size, (eggs)	No. clutches	Spawning interval (days)	*EPR*, Mean ± SD (egg female^{-1} day^{-1})	*SEPR* (% day^{-1})	Total number of eggs (*n*) produced during experiment, (egg female^{-1})	Maximum *n* per female mass (%)
ARK IX/4										
51a	25 August 1995	10	10	1–2	1–4	1–3	0.28 ± 0.18	0.22 ± 0.14	1–7	5.44
55	29 August 1995	14	17	1–2	1–6	1–4	0.25 ± 0.18	0.20 ± 0.14	1–10	7.78
75	05 September 1995	13	10	1–4	1–6	1–4	0.44 ± 0.26	0.34 ± 0.20	1–10	7.78
ARK XIII										
58	05 July 1997	1	27	1–2	8	1–4	0.44	0.35	12	9.33
59	06 July 1997	3	27	1–2	3–7	1–4	0.30 ± 0.13	0.23 ± 0.10	5–12	9.33
67	15 July 1997	4	20	1–2	2–3	1–4	0.19 ± 0.06	0.15 ± 0.05	2–5	4.67
79	21 July 1997	2	14	1–2	2–3	2–4	0.25	0.19	3–4	3.11
84	25 July 1997	2	8	1–2	1–3	1–3	0.31	0.25	1–4	3.11

Table 6 Egg volume, female dry mass (DM, number of measurements in brackets) and egg and female mass in carbon

Species	Egg volume (μm^3)	Egg mass (μg C)	Clutch mass (μg C)	Female mass (mg DW)	Female mass (mg C)	Clutch mass/female mass (%)
Egg-brooders						
Chiridius obtusifrons	12.8	1.79	66.2	0.81 ± 0.12 (12)[a]	0.36	18.4
Aetideopsis minor	8.95	1.25	11.9	0.31 ± 0.038 (4)[b]	0.14	8.5
Aetideopsis rostrata	11.7	1.64	21.9	0.55 ± 0.13 (13)[a]	0.25	8.8
Paraeuchaeta glacialis	79.9	11.2	802	7.96 ± 0.27 (3)[c]	3.58	22.4
Paraeuchaeta barbata	205.5	28.8	410.4	9.22 ± 1.49 (14)[d]	4.15	9.9
Paraeuchaeta polaris	206.0	28.8	167.0	3.47 ± 0.15 (2)[d]	1.56	10.7
Augaptilus glacialis	43.2	6.04	18.1	No data	0.20	9.1
Euaugaptilus hyperboreus	159.8	25.14	75.4	No data	0.86	8.8
Broadcast spawners						
Gaetanus tenuispinus	15.9	2.23	26.1	0.51 ± 0.14 (18)[a]	0.23	11.3
Gaetanus brevispinus	44.6	6.24	27.5	0.94 ± 0.21 (18)[a]	0.42	6.5
Heterorhabdus norvegicus	1.85	0.26	24.4	0.43 ± 0.12 (9)[a]	0.19	12.8
Spinocalanus horridus	5.76	0.81	6.8	No data	0.034	19.9
Scaphocalanus acrocephalus	25.1	3.5	7.03	1.00 ± 0.12 (9)[a]	0.45	1.6
Tharybis groenlandica	2.30	0.32	0.64	No data	0.023	2.8

For calculation details, see Methods

[a] Original DM measurements

[b] DM from Mizdalski (1988)

[c] DM from Auel and Hagen (2005)

[d] DM from Auel (1999)

Table 7 Reproductive modes in planktonic and benthopelagic aetideids

Species	Life style	Reproductive mode	Source
Gaetanus tenuispinus	Planktonic	Free spawning	This study
G. brevispinus	Planktonic	Free spawning	This study
G. minutus	Planktonic	Free spawning	Yamaguchi and Ikeda (2000) (=*Gaidius variabilis*)
G. intermedius	Planktonic	Free spawning	R. R. Hopcroft, unpublished data
Euchirella messinensis	Planktonic	Egg-brooding	Mauchline (1988)
E. bimudata	Planktonic	Egg-brooding	Mauchline (1988)
E. pseudopulchra	Planktonic	Egg-brooding	Mauchline (1988)
Pseudochirella obtusa	Planktonic	Egg-brooding	Ohman and Townsend (1998)
Chiridius obtusifrons	Planktonic	Egg-brooding	This study
C. gracilis	Planktonic	Egg-brooding	MacLellan and Shih (1974)
Aetideopsis minor	Planktonic	Egg-brooding	This study
A. rostrata	Benthopelagic (?)	Free spawning	This study
A. armata	Benthopelagic	Free spawning	Matthews (1964) (=*Chiridius armatus*)
Aetideus armatus	Benthopelagic	Free spawning	Matthews (1964)
Bradyidius armatus	Benthopelagic	Free spawning	Matthews (1964) (=*Bradyidius bradyi*)

e.g. in *Chiridius obtusifrons* (Figs. 3, 6). Adhesive membrane covering egg strings were also observed in the planktonic *Euchirella pseudopulchra* (Ohman and Townsend 1998). The outer membrane of *Gaetanus* eggs seems also to be adhesive, as the eggs stuck to the water surface and sides of experimental vials during our observations. In eggs of the two *Gaetanus* species here, conspicuous features were the double membrane and the perivitelline space which were also found in the congener species, *G. minutus* (A. Yamaguchi, personal communication) and *G. intermedius* (R. R. Hopcroft,

unpublished data). A significant increase of the egg volume within several hours after the egg laying may be considered as an adaptation for flotation at a particular depth. Observations of buoyant calanoid eggs also exist for *Calanus hyperboreus* (Conover 1988), *C. propinquus* (Kosobokova 1994), *C. glacialis* (Werner and Hirche 2001) and *Neocalanus* species (Saito and Tsuda 2000).

The variety of reproductive adaptations, and presence of both reproductive modes, in the Aetideidae is consistent with the plesiomorphic state of some mor-

phological characters in this family (Bradford-Grieve 2004). Furthermore, several features in aetideids suggest that some deep-sea genera are older than the pelagic ones, and that the benthopelagic environment was first invaded in deep waters (Bradford-Grieve 2004). As all the benthopelagic genera are free-spawning, it is tempting to conclude that the evolution of this reproductive behaviour, together with development of true egg sacs and floating eggs of the *Gaetanus* type, was fostered by the occupation of the pelagic environment. One might also speculate that the membranes covering the egg sacs in egg-brooding aetideids, and the outer membrane of *Gaetanus* eggs, have developed from the adhesive substance covering eggs of their benthopelagic ancestors. This adhesive substance seems to be a typical feature of the family, however, little is known about its composition and formation.

The other families studied here (Heterorhabdidae, Spinocalanidae, Scolecitrichidae, Tharybidae and Bathypontiidae) are presumably broadcast spawners. Although we observed egg laying directly only in one species from each of them, we base our conclusion on the fact that the members of these families were never observed carrying egg sacs nor remains of sacs attached to the genital somite.

Egg sac cover

The presence of true egg sacs and an envelope, or membrane enclosing the egg sacs in egg-brooding calanoids is under dispute. Huys and Boxshall (1991) doubted their presence after they failed to reveal an enclosing egg sac membrane in egg-carrying *Eurytemora velox*. In their diagnosis of the order, they stated "it is possible that true egg sacs do not occur within calanoida" (Huys and Boxshall 1991). Presumably following them, Mauchline (1998) also postulated that "the egg mass is often called an egg sac, but in calanoids there is no evidence that the eggs are contained in a membrane. Rather, the secretions that form the outer membrane of eggs of free spawners seem to be more copious in egg mass carriers so that the eggs as they are laid do not separate, but form into a mass attached to the genital somite" (p.267, Mauchline 1998).

Contrary to these conclusions, our observations provide clear evidence of the presence of enclosing egg sac membranes in the Euchaetidae, Augaptilidae and several Aetideidae. These observations are in accordance with the original observations by Hopkins (1976, 1977) who proved histologically the presence of an outer egg sac membrane surrounding the egg masses in *Paraeuchaeta norvegica* and concluded that this species does have an egg sac as defined by Corkett and McLaren (1969). The best visible part of egg sac membranes in the studied species is the upper (anterior) end of the sac where it is attached to the genital somite of the female (Fig. 5). The membranes were also easy to see around the lateral and posterior sides of the egg masses (Figs. 4, 5).

As to the formation of such membranes, an observation on a freshwater calanoid *Helidiaptomus viduus* suggested that there are special glands responsible for production of the extracellular envelops around the released eggs (Altaff and Chandran 1994). This thicker-walled and multicellular region at the posterior end of the *H. viduus* oviduct forms an elastic sac within itself filled with secretory material (Altaff and Chandran 1994). When the oviduct contained previtellogenic oocytes, the elastic sac was found attached throughout the inner wall of the oviducal gland. When the oocytes became fully developed, the elastic sac detached from the wall of the oviduct and released into the distal part of the oviduct in the genital segment. After fertilization of eggs, the elastic sac transformed into an ovisac, in which eggs were enclosed. Histochemical tests indicated the direct involvement of the elastic sac secretion in the formation of the ovisac (Altaff and Chandran 1994). The occurrence of such a gland had been previously reported for some cirripeds (Adiyodi and Anil Kumar 1988). To our knowledge, such glands have yet to be confirmed in marine calanoids.

Egg and brood size

The eggs of large deep-water euchaetid egg brooders are easy to collect, enumerate and measure. Therefore data on egg and clutch size are available for quite a number of species of this family (Bakke 1977; Hopkins 1977; Ward and Robins 1987; Mauchline 1995, 1998; Auel 2004). Mauchline (1998) showed that in 28 euchaetid species the egg diameter ranged from 200 to 870 mm, and clutch size from 5 to 60 eggs female^{-1}. He suggested that the same clutch range may apply to egg-brooders in general. From studies of 12 congeneric *Euchaeta* species partitioning the 2,500 m water column of the Rockall Trough, northeastern Atlantic Ocean, he concluded that the egg diameter tends to increase with depth, although brood size or volume does not (Mauchline 1994, 1995). The clutches of most of our egg-brooding species fell within the range of the Euchaetidae (Table 3) with *Paraeuchaeta glacialis* the only exception. In this species, clutch size ranged from 54 to 82 eggs with a mean of 71.7 eggs, far above the upper limit indicated by Mauchline (1998). The closer

to epipelagic habitat of *P. glacialis* presumably provides this species with abundant prey during the productive summer periods, with such resources transformed into large clutch sizes.

In broadcast spawners the number of eggs per clutch generally varies from 3 to 50, according to Mauchline (1998). Other studies frequently report on more than this for epipelagic species during the spring bloom (e.g. Hirche 1989, 1990; Kosobokova and Hirche 2001; Hirche and Kosobokova 2003; Hopcroft et al. 2005). During this study, we also observed a wider range in deep-dwelling species, from 1 to 95 eggs.

Reproductive investments

Reproductive investment standardized to female carbon mass can be informative, but lack of the temporal dimension to egg production makes comparison between species difficult. The broad variation of reproductive investments found during the present study (Table 6) arose partly because some species were able to produce small consecutive clutches at short intervals during a certain period, while others produced only one large clutch during the same period. Thus, *Scaphocalanus acrocephalus*, invested only 1.6% of female carbon in each clutch of two eggs (Table 6), but during 27 days its investment rose to 9.6% as clutches were produced almost every second day (Table 5)—comparable to the similar-sized arctic species *Calanus glacialis* (Hirche 1989). *Gaetanus* species were reported to produce up to five consecutive clutches with spawning intervals of 5–19 days at 5°C (Yamaguchi and Ikeda 2000). In egg brooding species, spawning intervals are presumably longer, as females carry egg sacs until nauplii hatch (e.g. Hopkins 1977; Alonzo et al. 2000b), and consecutive clutches are only possible with intervals longer than egg hatching time. Thus, in *Paraeuchaeta norvegica*, the average egg hatching time at 10°C was estimated as 18.7 days, and time to production of a new clutch as 22.3 days (Hopkins 1977). In *P. antarctica* eggs hatched 23.7 days after deposition of the sac, and the mean time taken by females to produce egg sacs was 21.5 days after appearance of developing eggs in oviducts at 2°C (Alonzo et al. 2000b). Finally, in *P. elongata* eggs hatched 39.4 days after deposition of the sac at 0.5°C (Ikeda and Hirakawa 1996). The production of consecutive clutches by *Paraeuchaeta* species in the Arctic presumably takes place at even longer intervals, taking into account lower ambient temperatures.

The reproductive investments of the Euchaetidae assessed by other authors in terms of DM are close to our estimates for *Paraeuchaeta glacialis* (Table 6).

Thus, for *P. norvegica* Hopkins (1977) reports 25%, and Båmstedt (1979) 37% of female DM invested in one clutch, while Ward and Robins (1987) assess it as 15–20% of DM for *P. antarctica*. In contrast to this, reproductive investments of the three *Paraeuchaeta* species and *Chiridius obtusifrons* assessed by Auel (2004) in terms of energy investment (in calories) were 2.3 times higher than our values (Table 6). They were estimated as 23.1% for *P. barbata*, 24.5% for *P. polaris*, 81.5% for *P. glacialis* and 41.7% for *C. obtusifrons* (Auel 2004). A major source of discrepancy is likely a significant overestimation of egg DM through use of the lyophilisation method and unrealistic lipid content of eggs (e.g., 93.7% for *P. polaris* eggs) used in calculations (Auel 2004).

Relation between egg and female size

The relation between egg and female size in marine planktonic copepods was analysed by Mauchline (1988), Kiørboe and Sabatini (1994, 1995,) Hopcroft and Roff (1998) and Ohman and Townsend (1998). Two different regression lines were suggested to scale egg size with body size of broadcasting and egg-brooding copepods (Kiørboe and Sabatini 1995; Ohman and Townsend 1998). Both regressions were almost entirely based on observations on epipelagic species. When combining our measurements with existing data sets (Ohman and Townsend 1998), our egg-brooders fit well to the regression for the other egg-brooders (Fig. 7). At the same time, the values for all broadcast spawners in this study except *Heterorhabdus norvegicus* better fit the regression for egg-brooders rather than broadcast spawners (Fig. 7). This indicates that deep-water broadcast spawners generally produce larger eggs compared to surface-dwelling broadcast spawning species. One might speculate that this larger egg size permits a reduction, or elimination of feeding during naupliar stages, thereby improving the survival potential of deep-water species. As the results for *H. norvegicus* match the data for epipelagic species we assume that nauplii in this species feed during their development like most epipelagic species.

A valid question then becomes how large need an egg to be for at least some young stages to develop without feeding? In the genus *Neocalanus*, *N. cristatus* nauplii (egg diameter 374 μm) do not feed to CI, while nauplii of *N. plumchrus* and *N. flemingeri* (egg diameter 150 μm) do beginning at NIII (Saito and Tsuda 2000; R. R. Hopcroft, unpublished data). Within the genus *Calanus*, *Calanus hyperboreus* (egg diameter 190 μm) is thought to have non-feeding nauplii to NIV (Mauchline 1998) while in smaller species *C. helgo-*
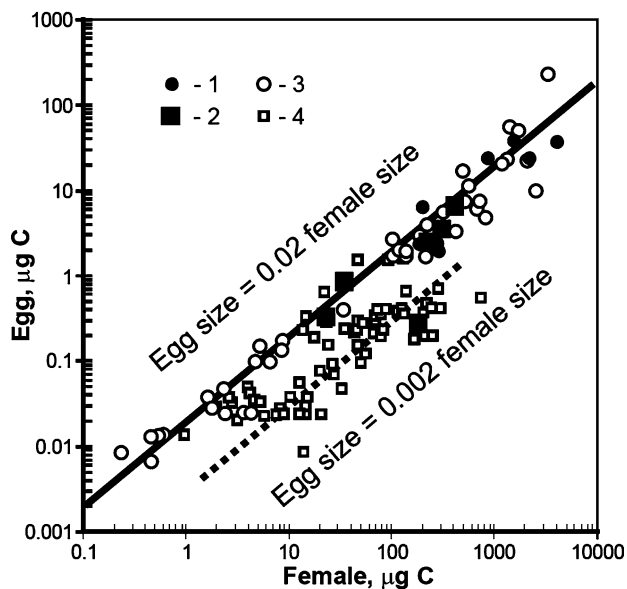
Fig. 7 Relationship between egg size and adult female body size for marine calanoid and cyclopoid copepods. *1* Egg-brooding Arctic deep-water species. *2* Broadcast-spawning Arctic deep-water species. *3* Egg-brooding species, after Ohman and Townsend (1998). *4* Broadcast-spawning, after Ohman and Townsend (1998)

landicus, *C. finmarchicus* and *C. glacialis* (egg diameter 173, 146 and 175 μm, respectively) nauplius III is the first feeding stage (Green et al. 1992). The naupliar stages of *Paraeuchaeta norvegica* (egg diameter 421 μm) do not feed (Nicholls 1934), and have none of the setae which Gauld (1959) found to be principally concerned with feeding in other species examined. Similarly, *P. elongata* nauplii do not appear to feed (Ikeda and Hirakawa 1996). In the bathypelagic *P. barbata* the egg store seems to be big enough for all naupliar stages and one or two copepodite stages to develop without feeding, as nauplii and copepodids CI and CII were found to have similar DM values, and DM started to increase only with CIII on (Auel and Hagen 2005). Adequate food stores require large eggs and hence numerically smaller broods which is apparently the pattern of adaptation for the bathypelagic *P. barbata* and *P. polaris* and the augaptilids *Augaptilus glacialis* and *Euaugaptilus hyperboreus*.

Despite the advances in knowledge during this study, for the majority of deep-water copepod species basic information on reproductive strategies and fecundity remains unavailable. Information on rates and processes, remains even more fragmentary and is insufficient to make general conclusions. Such information on reproductive biology and adaptations could be used as taxonomical characters and along with molecular techniques may help in interpretation of copepod phylogeny and evolutionary questions, as well as establish there basic productivity.

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