

M. Graeve · I.S. Wehrtmann

Lipid and fatty acid composition of Antarctic shrimp eggs (Decapoda: Caridea)

Received: 11 June 2002 / Accepted: 29 August 2002 / Published online: 26 October 2002
© Springer-Verlag 2002

Abstract Eggs of the decapod shrimps, *Chorismus antarcticus*, *Nematocarcinus lanceopes* and *Notocrangon antarcticus* were taken to analyse their morphometric, lipid and fatty acid composition. Almost all females carried undifferentiated eggs (stage I). The average number of recently extruded eggs was lowest in *C. antarcticus* with 163 eggs, and highest in *Nematocarcinus lanceopes* with 1,220 eggs, while *Notocrangon antarcticus* produced on average 350 eggs. The lipid content (% of dry mass) of the eggs was 18.8% for *C. antarcticus*, 14.3% for *Notocrangon antarcticus* and 18.1% for *Nematocarcinus lanceopes*. Dominant lipid classes in eggs of all species were phospholipids and triacylglycerols. The storage lipid, triacylglycerol, was slightly elevated in the eggs of *Nematocarcinus lanceopes* (mean of 52.7%) compared to the other two species. The fatty acid compositions of the decapod eggs were similar in the three species. Dominant fatty acids were 20:5(*n*-3), 18:1(*n*-9), 16:1(*n*-7), 16:0 and 18:1(*n*-7), comprising 75.8–78.4% of total fatty acids. Among the species, the eggs of *C. antarcticus* had the highest proportions of polyunsaturated fatty acids (39.6%), dominated by 20:5(*n*-3), and the lowest percentage of monounsaturates (41.8%). The eggs of *Nematocarcinus lanceopes* and *Notocrangon antarcticus* contained almost the same proportion of polyunsaturated fatty acids (28.0% and 28.4%, respectively), whereas *Nematocarcinus lanceopes* had the highest amount of monounsaturates due to the dominance of 18:1(*n*-9). Based on our findings, we assume that eggs produced by polar decapod crustaceans do not contain substantially more lipids than related species

from temperate or tropical regions. However, additional studies are necessary to substantiate any general conclusion about the relationship of egg lipid content and composition with climatic zones.

Introduction

Organisms inhabiting the Antarctic ecosystem have to cope with extreme conditions, especially constant low temperatures and pronounced seasonal food availability (e.g. Clarke 1979, 1983). Energy-demanding periods of their life cycle, such as production of eggs, embryogenesis and larval development (Clarke 1977a, b; Anger 1991 and references therein) need to be closely tied with the availability of adequate energy sources. Lipids are important fuel for marine organisms, especially for those living in high latitudes (e.g. Clarke 1983).

Although proteins are the main component of the eggs in marine invertebrates (Holland 1978), lipids play a central role in the embryonic metabolism. They represent the most important energy source and cover at least 60% of the total energy expenditure of the developing crustacean embryo (Herring 1974; Holland 1978; Amsler and George 1984). Furthermore, lipids provide structural components for membranes in the form of phospholipids (e.g. Sargent and Whittle 1981; Farkas et al. 1988). The lipid content of eggs of caridean decapods depends on their size, and was estimated at 6–9% and 37–39% of wet mass for small and large eggs, respectively (Herring 1974 and references therein). The relationship between clutch size and egg size may reflect the developmental mode and serves as an indicator of the energy content of the eggs (Herring 1974; Jaekle 1995). Triacylglycerols dominate the larger eggs and phospholipids the smaller ones (Herring 1974; Clarke 1977a, b; Kattner et al. 1994).

Wehrtmann and Graeve (1998) found a substantially higher amount of lipids in eggs of tropical benthic shrimps compared to benthic caridean shrimps of

M. Graeve (✉)
Alfred-Wegener-Institut für Polar- und Meeresforschung,
Am Handelshafen 12, 27570 Bremerhaven, Germany
E-mail: mgraeve@awi-bremerhaven.de
Tel.: +49-471-48311427
Fax: +49-471-48311425

I.S. Wehrtmann
Universidad de Costa Rica, Escuela de Biología,
2060 San Pedro-San José, Costa Rica

temperate waters. They deduced that a relationship exists between egg lipid deposition and latitude. However, data on lipid content of Antarctic shrimps are scarce. Clarke (1977b) reported on lipid and fatty acid data of eggs of *Chorismus antarcticus* (Pfeffer 1887); freshly spawned eggs contained 24% lipid per dry mass, consisting of 57% triacylglycerols and 43% phospholipids. These values are in accordance with values found for tropical shrimps (Wehrtmann and Graeve 1998). In this study, we report on lipid content and lipid and fatty acid composition of the eggs of three common Antarctic caridean shrimps: *C. antarcticus*, *Nematocarcinus lanceopes* (Bate 1888) and *Notocrangon antarcticus* (Pfeffer 1887). The results are compared with those reported for benthic caridean shrimps inhabiting other climatic zones, to obtain more insights into the relationship between egg lipid content and latitude.

Materials and methods

Egg-bearing females of the caridean shrimps, *C. antarcticus*, *Nematocarcinus lanceopes* and *Notocrangon antarcticus* were collected during the expedition of RV "Polarstern" ANT XV/3 (13 January to 28 March 1998) to the southern Weddell Sea and the Antarctic Peninsula. Detailed information concerning the cruise and the location of the study area has been published by Arntz and Gutt (1999). Animals were caught with an Agassiz trawl or a bottom trawl between 62°16' S; 58°43' W and 79°48' S; 08°25' W.

The animals were immediately sorted into species. The embryonic state was determined under a compound microscope according to the following criteria proposed by Wehrtmann (1990). Stage I: eggs recently produced; uniform yolk; no eye pigments visible. Stage II: eye pigments barely visible. Stage III: eyes clearly visible and fully developed; abdomen free. Before removing the eggs, we measured the carapace length (CL) of the female shrimps from the eye socket to the rear of the carapace in the mid-dorsal line. Oviparous females of each species were stored in formaldehyde (10%) immediately after sorting. In the home laboratory, the length and width of 15 eggs per female were measured with a microscope equipped with a calibrated ocular micrometer. Individual egg volume (V) was calculated using the formula for oblate spheroids provided by Turner and Lawrence (1979). The egg mass was separated from the female, counted, rinsed with distilled water, and interstitial water was removed using filter paper. For dry mass determination, the egg samples were oven-dried (50°C) until constant weight was attained (ca. 28 h).

For lipid analyses, all embryos were removed from each female, counted, and stored in separate glass tubes filled with a mixture of dichloromethane:methanol (2:1; v:v). These samples were deposited at -25°C until lipid analyses. The eggs were homogenised and extracted in dichloromethane:methanol (2:1; v:v) according to Folch et al. (1957). The lipid class compositions were determined according to Fraser and Tocher (1985) by thin-layer chromatography-flame ionisation detection (TLC-FID) with an IATROSCAN Mark IV TH 10. Commercial and natural standard mixtures (e.g. from copepods or fish oil) of different lipid classes (phospholipids, triacylglycerols, sterols, wax esters) were used for identification (Hagen 1988).

For the gas-liquid chromatographic analysis of the fatty acids, aliquots of the extracted samples were taken. Methyl esters of fatty acids were prepared by transesterification with 3% concentrated sulphuric acid in methanol for 4 h at 80°C. An internal standard (19:0 fatty acid) was added for quantification. After their extraction with hexane, the fatty acid methyl esters were analysed with a gas-liquid chromatograph (Chrompack 9000) on a capillary column (30 m x 0.25 mm; film thickness: 0.25 µm; liquid phase: DB-FFAP)

using temperature programming according to the method proposed by Kattner and Fricke (1986). Fatty acids were identified with standard mixtures. Total lipid is defined as the sum of all fatty acids, which is a slight underestimate of the real value.

Results

Egg production and egg composition

The mean carapace length of ovigerous females was 16.9 mm (± 1.12 mm SD; $n=5$), 21.7 mm (± 1.51 mm SD; $n=6$) and 26.3 mm for *C. antarcticus*, *Notocrangon antarcticus* and *Nematocarcinus lanceopes*, respectively. Almost all females carried undifferentiated eggs (stage I); however, embryos of one female of *Nematocarcinus lanceopes* were close to hatching (stage III). The average number of recently extruded eggs was lowest in *C. antarcticus* with 163 eggs (± 64 SD; $n=14$), and highest in *Nematocarcinus lanceopes* with 1219 eggs (± 64 SD; $n=6$); *Notocrangon antarcticus* produced on average 348 eggs (± 170 SD; $n=14$).

Table 1 summarises the data of biomass and water content of freshly laid eggs of the three species. The egg volume varied considerably among species. The smallest eggs were produced by *Nematocarcinus lanceopes* (mean of 1.2 mm³), and the largest by *C. antarcticus* (mean of 3.1 mm³). Average egg volume in *Notocrangon antarcticus* was 2.0 mm³. Average dry mass of the egg batch was elevated in *Notocrangon antarcticus* and *Nematocarcinus lanceopes* (239 and 338 mg, respectively) while it was substantially lower in *C. antarcticus* (135 mg). However, average dry mass per egg was highest in the last species (830 µg) and lowest in *Nematocarcinus lanceopes* (277 µg). Despite these interspecific differences, the water content of the eggs was similar among species, and ranged from 67% to 72%.

Lipid class and fatty acid composition

The egg lipid content (% of dry mass) was estimated for *C. antarcticus* with 18.8%, for *Notocrangon antarcticus* with 14.3%, and for *Nematocarcinus lanceopes* with 18.1% (Table 1). Dominant lipid classes in newly spawned eggs of all species were phospholipids and triacylglycerols (Table 1). The storage lipids, triacylglycerols, were slightly elevated in the eggs of *Nematocarcinus lanceopes* (mean of 52.7%) compared to the other two species. Eggs of *C. antarcticus* exhibited almost equal proportions of triacylglycerols and phospholipids, with 48.4% and 46.3%, respectively. An enhanced proportion of phospholipids (53.2%) was found in recently extruded eggs of *Notocrangon antarcticus*. Sterols occurred in small amounts in *C. antarcticus* and *Notocrangon antarcticus* (2.4% and 2.5%, respectively), and were slightly elevated in eggs produced by *Nematocarcinus lanceopes* (4.2%) (Table 1).

Table 1 Biomass, water content and lipid class composition of recently extruded eggs (stage I) by *Chorismus antarcticus*, *Notocrangon antarcticus* and *Nematocarcinus lanceopes* (TAG triacylglycerols; PL polar lipids)

	Mean	SD	Minimum	Maximum	N
<i>Chorismus antarcticus</i>					
Egg volume (mm ³)	3.1	±0.5	2.6	3.6	14
Dry mass/clutch (mg)	135	±71	64	206	6
Dry mass/egg (µg)	830	±73	757	903	6
Water content (%)	72	±4	65	76	6
Total fatty acids of egg (µg)	156	±29	127	185	9
Egg lipid content (% lipid of dry mass)	18.8				
TAG (% of total lipids)	48.4	±7.6			
PL (% of total lipids)	46.3	±8.2			
Sterols (% of total lipids)	2.5	±2.6			
<i>Notocrangon antarcticus</i>					
Egg volume (mm ³)	2.0	±0.5	1.5	2.5	11
Dry mass/clutch (mg)	239	±99	138	338	6
Dry mass/egg (µg)	687	±27	660	714	6
Water content (%)	67	±1	66	68	6
Total fatty acids of egg (µg)	99	±12	87	111	4
Egg lipid content (% lipid of dry mass)	14.3				
TAG (% of total lipids)	42.1	±3.6			
PL (% of total lipids)	53.2	±4.7			
Sterols (% of total lipids)	2.4	±1.6			
<i>Nematocarcinus lanceopes</i>					
Egg volume (mm ³)	1.2	±0.3	0.9	1.5	6
Dry mass/clutch (mg)	338	–	–	–	1
Dry mass/egg (µg)	277	–	–	–	1
Water content (%)	70	–	–	–	1
Total fatty acids of egg (µg)	50	±13	37	63	5
Egg lipid content (% lipid of dry mass)	18.1				
TAG (% of total lipids)	52.7	±10.1			
PL (% of total lipids)	41.5	±9.2			
Sterols (% of total lipids)	4.2	±1.7			

The dominant fatty acids of the shrimp eggs were 20:5(*n*-3), 18:1(*n*-9), 16:1(*n*-7), 16:0 and 18:1(*n*-7). Despite the general similarity, the proportions of the individual fatty acids were partially different (Table 2). Main components in eggs of *C. antarcticus* were 20:5(*n*-3), 18:1(*n*-9) and 16:0 fatty acids (ranked in descending order), composing 52.5% of the total fatty acids. The

eggs of this species had the highest proportion of polyunsaturated fatty acids (39.6%), dominated by 20:5(*n*-3), and the lowest proportion of monounsaturated fatty acids (41.8%). In *Nematocarcinus lanceopes* eggs, the average proportion of monounsaturates was highest (56.3%). The predominant fatty acid was 18:1(*n*-9) (26.3%), as well as 16:1(*n*-7) and 20:5(*n*-3). Major fatty

Table 2 Fatty acid composition (mass percent of total fatty acids with standard deviation, *SD*) of recently extruded eggs of *Chorismus antarcticus* (*n* = 10), *Notocrangon antarcticus* (*n* = 5) and *Nematocarcinus lanceopes* (*n* = 6) (– < 0.5% or not detected)

Fatty acids	<i>Chorismus antarcticus</i>		<i>Notocrangon antarcticus</i>		<i>Nematocarcinus lanceopes</i>	
	Mass%	SD	Mass%	SD	Mass%	SD
14:0	2.4	±0.3	2.3	±0.1	2.8	±0.3
15:0	0.7	±0.2	0.6	±0.1	–	–
16:0	14.2	±2.1	15.2	±2.0	11.9	±1.1
16:1(<i>n</i> -7)	13.1	±2.4	18.7	±5.6	17.7	±3.0
16:3	0.8	±0.1	1.0	±0.3	0.8	±1.0
18:0	1.3	±0.2	1.5	±0.1	0.8	±0.1
18:1(<i>n</i> -9)	15.5	±3.2	16.9	±1.4	26.3	±2.5
18:1(<i>n</i> -7)	10.9	±1.9	12.8	±2.1	8.5	±0.6
18:2(<i>n</i> -6)	1.7	±0.2	1.5	±0.2	4.1	±5.2
18:3(<i>n</i> -3)	0.6	±0.2	0.6	±0.1	0.6	±0.0
18:4(<i>n</i> -3)	1.4	±0.6	1.2	±1.2	0.9	±0.2
20:1(<i>n</i> -9)	1.0	±0.5	1.5	±0.3	1.6	±0.6
20:1(<i>n</i> -7)	0.5	±0.3	1.6	±0.2	0.6	±0.1
20:4(<i>n</i> -6)	3.1	±0.7	2.7	±0.7	1.1	±0.2
20:4(<i>n</i> -3)	0.6	±0.2	4.5	±6.6	–	±0.2
20:5(<i>n</i> -3)	22.8	±4.4	12.2	±7.8	14.0	±1.9
22:1(<i>n</i> -11)	–	–	–	–	1.1	±1.6
22:5(<i>n</i> -3)	0.8	±0.5	0.5	±0.5	–	–
22:6(<i>n</i> -3)	7.4	±4.2	4.2	±4.3	5.8	±2.9
Σ Saturates	18.6		19.6		15.5	
Σ Monounsats.	41.0		51.5		55.8	
Σ Polyunsats.	39.6		28.4		27.3	

acids of *Notocrangon antarcticus* eggs were 16:1(*n*-7), 18:1(*n*-9) and 16:0. This species had the highest proportion of saturates (19.6%). The eggs of *Nematocarcinus lanceopes* and *Notocrangon antarcticus* contained almost the same proportion of polyunsaturated fatty acids (28.0% and 28.4%, respectively).

Discussion

Egg production and egg composition

Females of *C. antarcticus*, *Notocrangon antarcticus* and *Nematocarcinus lanceopes* collected for our egg-composition studies carried mostly undifferentiated eggs. Carapace length and egg numbers are in the general range reported for these species (Gorny et al. 1992). However, egg dry masses of the three species were lower and egg volumes of *C. antarcticus* and *Notocrangon antarcticus* slightly higher than those reported by Clarke (1993). He analysed egg size and egg composition of polar shrimps, including the three caridean shrimps studied here (egg-volume data were not available for *Nematocarcinus lanceopes*). Such plasticity concerning reproductive aspects is a common feature among decapods (e.g. Jones and Simons 1983; Giménez and Anger 2001).

The relationships between interpopulational egg variability and latitudinal gradients have been studied in several caridean shrimps inhabiting the southern hemisphere (Gorny et al. 1992, 1993; Wehrtmann and Kattner 1998; Wehrtmann and Lardies 1999; Lardies and Wehrtmann 2001). Since our egg dry-mass data for the three species are lower than those reported by Clarke (1993), we assume that these intraspecific differences are related to year-to-year variation.

Generally, marine demersal eggs, which release planktonic larvae, have a considerably lower water content than marine planktonic eggs, which also produce planktonic larvae (Pandian 1970). The water content of recently extruded eggs of marine benthic decapods with planktonic larvae is around 50–60%, reaching 70–80% at the end of the incubation period (Pandian 1970). Published values for freshly laid eggs of caridean shrimps from central-southern Chile [*Betaeus emarginatus*: 57% (Lardies and Wehrtmann 1997); *B. truncatus*: 55% (Lardies and Wehrtmann 2001); *Nauticaris magellanica*: 50% (Wehrtmann and Kattner 1998)] lie within this range. As in the pandalid shrimp *Austropandalus grayi*, collected in the Magellan region of South America [stage I eggs: 62% (Wehrtmann and Lardies 1999)], the water content of freshly laid eggs of the three Antarctic shrimps studied was slightly higher than the 50–60% range (Pandian 1970). Although no data have been published concerning the water content of eggs produced by polar decapods, the values for eggs of caridean shrimps from the Magellan region and the present results from Antarctica seem to indicate that the water content is slightly elevated in shrimps inhabiting cold-water regions.

Lipid and fatty acid composition

The eggs of the three Antarctic caridean shrimp species had moderate lipid contents, mainly consisting of triacylglycerols and phospholipids. The dominance of only two lipid classes is typical for eggs of decapod crustaceans (Clarke 1977a, b, 1979; Clarke et al. 1990; Wehrtmann and Graeve 1998). Storage of wax esters induced by the highly seasonal food availability in high-latitude regions has not been observed (Clarke 1977b). Triacylglycerols are preferentially utilised during embryonic development (Clarke et al. 1990; Wehrtmann and Graeve 1998). The sum of triacylglycerols in relation to phospholipids varies with the physiological state, but the overall lipid pattern seems to be similar in many organisms, e.g. shrimps (Clarke 1977b; Hopkins et al. 1993), asteroids (Falk-Petersen and Sargent 1982), crabs (Mourente et al. 1994), gastropods and polychaetes (Parrish et al. 1996), and zooplankton and fish (Reinhardt and Van Vleet 1986). High proportions of lipids can decrease the density of the eggs considerably, and consequently the size/density/lipid relationship has a substantial effect on the developmental pattern of decapod shrimps (Herring 1974; Wehrtmann and Kattner 1998). However, since almost all eggs of the caridean shrimp species studied by us presented recently produced embryos, no conclusion could be drawn on triacylglycerol consumption during embryonic development.

The egg lipids of the three shrimp species consisted of fatty acids, which generally dominate the lipids of marine invertebrates: high proportions of polyunsaturated and monounsaturated fatty acids, as well as the saturate 16:0 (Clarke 1977a, b; Wehrtmann and Graeve 1998; Narcisco and Morais 2001). The fatty acid composition of *C. antarcticus* eggs is in good agreement with data reported by Clarke (1977b), although no such data exist for *Notocrangon antarcticus* and *Nematocarcinus lanceopes*. The same major fatty acids occurred in all species and resembled closely those of other decapod eggs (Clarke 1977a, b, 1979, 1993; Hopkins et al. 1993; Kattner et al. 1994; Graeve et al. 1997; Wehrtmann and Graeve 1998; Wehrtmann and Kattner 1998). However, the proportions of the fatty acids were different in the three species. In *C. antarcticus* eggs, 20:5(*n*-3) was clearly higher than in the other species; 20:5(*n*-3) usually originates from diatoms and is transferred through the food web (e.g. Fraser et al. 1989). This fatty acid might indicate feeding on diatom-influenced food, although the other predominant diatom fatty acid 16:1(*n*-7) did not support this assumption; 16:1(*n*-7) was even higher in the eggs of the two other species, with lower proportions of 20:5(*n*-3). The production of eggs is probably fuelled more directly through ingestion of lipids, as found in Arctic caridean shrimps, suggesting a dependence of egg production on sufficient food resources (Graeve et al. 1997).

Compared to the other species, *Nematocarcinus lanceopes* produces the smallest eggs but the highest

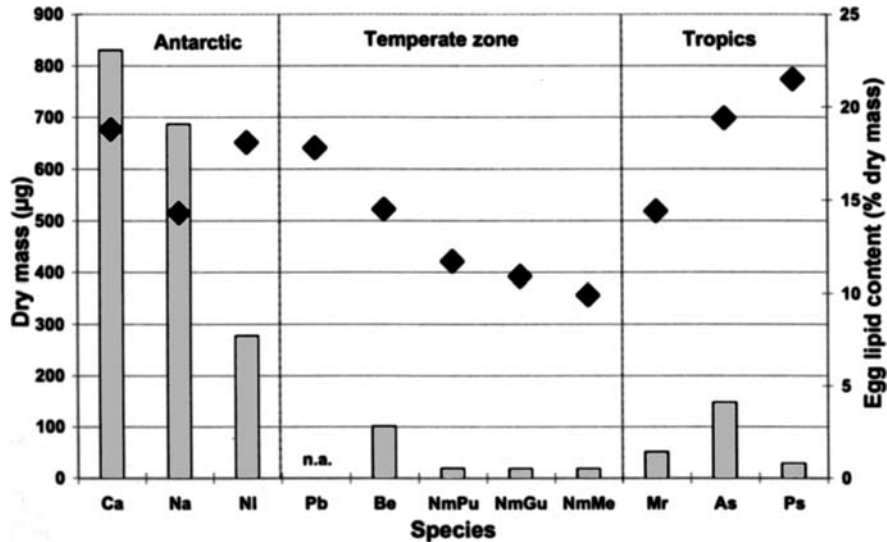


Fig. 1 Lipid content (diamonds; expressed as percent of egg dry mass) and average dry mass (grey bar; n.a. data not available) of recently extruded eggs of caridean shrimp species inhabiting different climatic zones; data are based upon the sum of total fatty acids (exception: *Macrobrachium rosenbergii*, where data represent total lipid content) [*Ca Chorismus antarcticus* (present study); *Na Notocrangon antarcticus* (present study); *NI Nematocarcinus lanceopes* (present study); *Pb Pandalus borealis* (from Hopkins et al. 1993); *Be Betaeus emarginatus* (egg lipid content: I.S. Wehrtmann and G. Kattner, unpublished data; dry mass data: Lardies and Wehrtmann 1997); *NmPu Nauticaris magellanica* from Putemún, southern Chile; *NmGu Nauticaris magellanica* from Guanqueros, northern Chile; *NmMe Nauticaris magellanica* from Metri, central-southern Chile (all from Wehrtmann and Kattner 1998); *Mr Macrobrachium rosenbergii* (from Clarke et al. 1990); *As Alpheus saxidomus*; *Ps Palamonetes schmitti* (both from Wehrtmann and Graeve 1998)]

number of eggs per clutch, in combination with the highest level of triacylglycerols and 18:1(*n*-9) fatty acid. This fatty acid is often a major component of storage lipids. However, it is speculative to conclude that this combination of lipid pattern with egg and clutch size is typical for small eggs of decapods. In general, we found no clear relationship of fatty acid composition with egg or clutch size, egg dry mass or lipid content or lipid class composition.

The fatty acid composition of the eggs of the shrimp species reflects in general a feeding behaviour where material sedimenting to the sea floor is ingested throughout the year. We found no clear indication of deviating food preferences or uptake between the species. This similarity is in contrast to other bottom-living invertebrates where fatty acid compositions have been shown to be very useful in elucidating feeding interactions (Graeve et al. 1997, 2001). Clear relationships have been also found between zooplankton growth, egg production and intake of polyunsaturated fatty acids (Jónasdóttir 1994; Müller-Navarra et al. 2000).

The total lipid content per clutch was similar in *C. antarcticus* and *Notocrangon antarcticus* but higher in *Nematocarcinus lanceopes*. The egg lipid content of these Antarctic species is comparable to that of tropical

shrimps, but slightly higher than in most decapod crustacean eggs from temperate zones (Wehrtmann and Graeve 1998; Wehrtmann and Kattner 1998) (Fig. 1). This is in contrast to most euphausiids, copepods and shrimps, which have a clear tendency to accumulate large lipid stores at high latitudes (Lee and Hirota 1973; Sargent and Whittle 1981; Clarke 1983, 1987; Sargent and Henderson 1986; Hagen 1988). It is also well known that eggs of polar marine invertebrates are usually larger than those of tropical species and richer in lipid (Clarke 1983 and references therein). Considering the study by Wehrtmann and Graeve (1998), we therefore expected a higher egg lipid content for Antarctic shrimps compared to tropical species. However, due to the limited number of polar species and the fact that the egg lipid content may vary inter- and intra-specifically (Herring 1974; Hopkins et al. 1993), we cannot point to a clear relationship between lipid content and climatic zone. The different methods used within the various studies to estimate the lipid content make it even more difficult to compare published data. Moreover, Clarke (1983) raised the question: “is polar benthos rich in lipids?”. Our findings lead us to the conclusion that there is no indication that eggs produced by polar decapod crustaceans contain substantially more lipid than related species from temperate or tropical zones. That conclusion is in clear contrast to findings on polar zooplankton, which is known to synthesise exceptionally large lipid stores (Lee et al. 1971; Lee and Hirota 1973; Lee 1974; Clarke 1983; Kattner and Hagen 1995). Additional data, especially from tropical and polar decapods, are required to substantiate general conclusions about relationships between egg lipid content and climatic zone.

Acknowledgements We are grateful to Bodil Bluhm (IARC, Fairbanks, USA) who was very co-operative in sharing her crustacean samples and provided data on carapace length. We also thank the master and crew of RV “Polarstern” for their professional support. Comments and suggestions of Gerhard Kattner, AWI, greatly improved the manuscript.

References

- Amsler MO, George RY (1984) Seasonal variation in the biochemical composition of the embryos of *Callinectes sapidus* Rathbun. *J Crust Biol* 4:546–553
- Anger K (1991) Developmental changes in the bioenergetics of decapod larvae. *Mem Queensl Mus* 31:289–308
- Arntz WE, Gutt J (eds) (1999) The Expedition ANTARKTIS XV/3 (EASIS II) of RV “Polarstern” in 1998. *Ber Polarforsch* 301:1–229
- Bate CS (1888) Report on the Crustacea *Macrura* dredged by “H.M.S. Challenger” during the years 1873–1876. Report on the scientific results of the voyage of “H.M.S. Challenger” during the year 1873–1876. *Zoology* 24:1–942
- Clarke A (1977a) Seasonal variations in the total lipid content of *Chorismus antarcticus* (Pfeffer) (Crustacea: Decapoda) at South Georgia. *J Exp Mar Biol Ecol* 27:93–106
- Clarke A (1977b) Lipid class and fatty acid composition of *Chorismus antarcticus* (Pfeffer) (Crustacea: Decapoda) at South Georgia. *J Exp Mar Biol Ecol* 28:297–314
- Clarke A (1979) Lipid content and composition of the pink shrimp *Pandalus montagui* (Leach) (Crustacea: Decapoda) at South Georgia. *J Exp Mar Biol Ecol* 38:1–17
- Clarke A (1983) Life in cold water: the physiological ecology of polar marine ectotherms. *Oceanogr Mar Biol Annu Rev* 21:341–453
- Clarke A (1987) Temperature, latitude and reproductive output. *Mar Ecol Prog Ser* 38:89–99
- Clarke A (1993) Egg size and egg composition in polar shrimps (Caridea: Decapoda). *J Exp Mar Biol Ecol* 168:189–203
- Clarke A, Brown JH, Holmes LJ (1990) The biochemical composition of eggs from *Macrobrachium rosenbergii* in relation to embryonic development. *Comp Biochem Physiol* 96B:505–511
- Falk-Petersen I-B, Sargent JR (1982) Reproduction of asteroids from Balsfjorden, northern Norway: analyses of lipids in the gonads of *Ctenodiscus crispatus*, *Asterias lincki* and *Pteraster militaris*. *Mar Biol* 69:291–298
- Farkas T, Storebakken T, Bhosle NB (1988) Composition and physical state of phospholipids in calanoid copepods from India and Norway. *Lipids* 23:619–622
- Folch J, Lees M, Sloane-Stanley GH (1957) A simple method for the isolation and purification of total lipides from animal tissues. *J Biol Chem* 226:497–509
- Fraser AJ, Tocher DR (1985) Thin-layer chromatography-flame ionization detection and quantification of marine neutral lipids and phospholipids. *J Exp Mar Biol Ecol* 88:91–100
- Fraser AJ, Sargent JR, Gamble JC, Seaton DD (1989) Formation and transfer of fatty acids in an enclosed marine food chain comprising phytoplankton, zooplankton and herring (*Clupea harengus* L.) larvae. *Mar Chem* 27:1–18
- Giménez L, Anger K (2001) Relationships among salinity, egg size, embryonic development, and larval biomass in the estuarine crab *Chasmagnathus granulata* Dana, 1851. *J Exp Mar Biol Ecol* 260:241–257
- Gorny M, Arntz WE, Clarke A, Gore DJ (1992) Reproductive biology of caridean decapods from the Weddell Sea. *Polar Biol* 12:111–120
- Gorny M, Brey T, Arntz W, Bruns T (1993) Growth, development and productivity of *Chorismus antarcticus* (Pfeffer) (Crustacea: Decapoda: Natantia) in the eastern Weddell Sea, Antarctica. *J Exp Mar Biol Ecol* 174:261–275
- Graeve M, Kattner G, Piepenburg D (1997) Lipids in Arctic benthos: does the fatty acid and alcohol composition reflect feeding and trophic interactions? *Polar Biol* 18:53–61
- Graeve M, Dauby P, Scaillteur Y (2001) Combined lipid, fatty acid and digestive tract content analyses: a penetrating approach to estimate feeding modes of Antarctic amphipods. *Polar Biol* 24:853–862
- Hagen W (1988) Zur Bedeutung der Lipide im antarktischen Zooplankton. *Ber Polarforsch* 49:1–129
- Herring PJ (1974) Size, density and lipid content of some decapod eggs. *Deep-Sea Res* 21:91–94
- Holland DL (1978) Lipid reserves and energy metabolism in the larvae of benthic marine invertebrates. In: Malins DC, Sargent JR (eds) *Biochemical and biophysical perspectives in marine biology*. Academic Press, London, pp 85–123
- Hopkins CCE, Sargent JR, Nilssen EM (1993) Total lipid content, and lipid and fatty acid composition of the deep-water prawn *Pandalus borealis* from Balsfjord, northern Norway: growth and feeding relationships. *Mar Ecol Prog Ser* 96:217–228
- Jaeckle WB (1995) Variation in the size, energy content, and biochemical composition of invertebrate eggs: correlates to the mode of larval development. In: McEdwards L (ed) *Ecology of marine invertebrate larvae*. CRC Press, Boca Raton, pp 49–77
- Jónasdóttir SH (1994) Effects of food quality on the reproductive success of *Acartia tonsa* and *Acartia hudsonica*: laboratory observations. *Mar Biol* 121:67–81
- Jones MB, Simons MJ (1983) Latitudinal variation in reproductive characteristics of a mud crab, *Helica crassa* (Grapsidae). *Bull Mar Sci* 33:656–670
- Kattner G, Fricke HSG (1986) Simple gas-liquid chromatographic method for the simultaneous determination of fatty acids and alcohols in wax esters of marine organisms. *J Chromatogr* 361:263–268
- Kattner G, Hagen W (1995) Polar herbivorous copepods – different pathways in lipid biosynthesis. *ICES J Mar Sci* 52:329–335
- Kattner G, Wehrtmann IS, Merck T (1994) Interannual variations of lipids and fatty acids during larval development of *Crangon* spp. in the German Bight, North Sea. *Comp Biochem Physiol* 107B:103–110
- Lardies MA, Wehrtmann IS (1997) Egg production in *Betaeus emarginatus* (H. Milne Edwards, 1837) (Decapoda: Alpheidae): fecundity, reproductive output and chemical composition of eggs. *Ophelia* 46:165–174
- Lardies MA, Wehrtmann IS (2001) Latitudinal variation in the reproductive biology of *Betaeus truncatus* (Decapoda: Alpheidae) along the Chilean coast. *Ophelia* 55:55–67
- Lee RF (1974) Lipids of zooplankton from Bute Inlet, British Columbia. *J Fish Res Board Can* 31:1577–1588
- Lee RF, Hirota J (1973) Wax esters in tropical zooplankton and nekton and the geographical distribution of wax esters in marine copepods. *Limnol Oceanogr* 18:227–239
- Lee RF, Hirota J, Barnett AM (1971) Distribution and importance of wax esters in marine copepods and other zooplankton. *Deep-Sea Res* 18:1147–1165
- Mourente G, Medina E, Gonzáles S, Rodríguez A (1994) Changes in lipid class and fatty acid contents in the ovary and midgut gland of the female fiddler crab *Uca tangeri* (Decapoda, Ocypodiidae) during maturation. *Mar Biol* 121:187–197
- Müller-Navarra DC, Brett MT, Liston AM, Goldman CR (2000) A highly unsaturated fatty acid predicts carbon transfer between primary producers and consumers. *Nature* 403:74–77
- Narcisco L, Morais S (2001) Fatty acid profile of *Palaemon serratus* (Palaemonidae) eggs and larvae during embryonic and larval development using different live diets. *J Crust Biol* 21:566–574
- Pandian TJ (1970) Ecophysiological studies on the developing eggs and embryos of the European lobster *Homarus gammarus*. *Mar Biol* 7:249–254
- Parrish CC, Yang Z, Lau A, Thompson RJ (1996) Lipid composition of *Yoldia hyperborea* (Protobranchia), *Nephtys ciliata* (Nephtyidae) and *Arctacama probscidea* (Terebellidae) living at sub-zero temperatures. *Comp Biochem Physiol* 114B:59–67
- Pfeffer G (1887) Die Krebse von Süd-Georgien nach der Ausbeute der deutschen Station 1882–83. 1. *Mitt Naturhist Mus Hamb* 4:42–150
- Reinhardt SB, Van Vleet ES (1986) Lipid composition of twenty-two species of Antarctic midwater zooplankton and fish. *Mar Biol* 91:149–159
- Sargent JR, Henderson RJ (1986) Lipids. In: Corner EDS, ÓHara SCM (eds) *The biological chemistry of marine copepods*. Clarendon Press, Oxford, pp 59–108

- Sargent JR, Whittle KJ (1981) Lipids and hydrocarbons in the marine food web. In: Longhurst A (ed) Analysis of marine ecosystems. Academic Press, London, pp 491–533
- Turner RL, Lawrence JM (1979) Volume and composition of echinoderm eggs: implications for the use of egg size in life-history models. In: Stancyk SE (ed) Reproductive ecology of marine invertebrates. The Belle W. Baruch Library in Marine Science no. 9. University of South Carolina Press, Columbia, pp 25–40
- Wehrtmann IS (1990) Distribution and reproduction of *Ambidexter panamense* and *Palaemonetes schmitti* in Pacific Costa Rica (Crustacea, Decapoda). Rev Biol Trop 38:327–329
- Wehrtmann IS, Graeve M (1998) Lipid composition and utilization in developing eggs of two tropical marine caridean shrimps (Decapoda: Caridea: Alpheidea, Palaemonidae). Comp Biochem Physiol B 112:457–463
- Wehrtmann IS, Kattner G (1998) Changes in volume, biomass, and fatty acids of developing eggs in *Nauticaris magellanica* (Decapoda: Caridea): a latitudinal comparison. J Crust Biol 18:413–422
- Wehrtmann IS, Lardies MA (1999) Egg production of *Austropandalus grayi* (Decapoda, Caridea, Pandalidae) from the Magellan region, South America. Sci Mar 63:325–331