



Changes in biomass, lipid, fatty acid and elemental composition during the abbreviated larval development of the subantarctic shrimp *Campylonotus vagans*

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Abstract

Ontogenetic changes in biomass and chemical composition were studied in the laboratory during the abbreviated larval and early juvenile development of the caridean shrimp *Campylonotus vagans* from the subantarctic Beagle Channel, Argentina. At 7 ± 0.5 °C, development from hatching to metamorphosis took about 44 days. The larvae started feeding on *Artemia* nauplii immediately after hatching, although larval resistance to starvation was high (average 18 days, maximum 29 days). Dry mass (DM), carbon (C), nitrogen (N) and hydrogen (H) contents increased about a fourfold from hatching to metamorphosis, while the C:N mass ratio increased from about 3.7 to 4.3. The protein and total lipid contents increased gradually from hatching to the first juvenile stage, the former from 190 to 640 µg/individual, the latter from 37 to 95 µg/individual. The lipid mass fraction was low throughout larval development (3–9% of DM), while the protein content was much higher and almost constant (30–40%). The dominating fatty acids were 18:1(n-9), 16:0, 20:5(n-3), 18:1(n-7), 18:3(n-3), 18:0, 16:1(n-7). Except for 20:5(n-3), these resulted mainly from food uptake (*Artemia* nauplii). Exuvial losses of C, H and N (all larval stages combined) accounted for only 7%, 1% and 1% of the initial values at hatching. In contrast, 37% of initial DM was lost. Partially food-independent

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(endotrophic) larval development is discussed as an adaptation to food scarcity at high latitudes, while the abbreviated planktotrophic larval development appears to be synchronised with seasonal peaks in primary production, allowing for an optimal resource exploitation in a food-limited environment.

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1. Introduction

On a macroecological scale, many marine invertebrate groups show a remarkable reduction in species diversity towards higher latitudes, probably best documented for marine bivalve molluscs (Crame, 1999, 2000a,b) and decapod crustaceans (Gorny, 1999). Both groups present a bell-shaped pattern with decreasing species diversity towards high latitudes. Among the decapods, only eight natant shrimp species have been found in the high Antarctic Weddell Sea (Arntz et al., 1992). Reptant crabs seem to be entirely absent from the high Antarctic shelf, although a few lithodid crab species have been found off the shelf, mostly at depths below 250 m (Klages et al., 1995; Arana and Retamal, 1999). In contrast, a high diversity of reptants has been recorded in cold-temperate areas of the subpolar regime (Gorny, 1999).

Strongly pronounced seasonality in planktonic food availability due to short periods of primary production is, besides low temperatures, presumably a major selective force in high latitudes (for discussion, see Clarke, 1987; Pearse et al., 1991; Knox, 1994). Species without a fully planktotrophic mode of larval development may thus have to adapt to such a food-limited conditions, synchronising their larval phase with short and pulsed primary production. However, the adaptability may be limited by physiological constraints associated with low temperatures, which cause slow development in both embryos and larvae (Clarke, 1982, 1983).

In the present study we have chosen the subantarctic caridean shrimp *Campylonotus vagans* Bate, 1888, as an example of early life history adaptations to strongly pulsed food availability. The family Campylonotidae shows several ecological and biogeographic patterns, which enable us to discuss our findings in a wider ecological context, and in relation to high Antarctic shrimp species. The Campylonotidae show a circumpolar distribution and consist of five representatives exclusively known from the Southern Ocean, one of which was recently discovered in Antarctic waters (Torti and Boschi, 1973; Thatje, 2003).

2. Materials and methods

2.1. Capture and maintenance of ovigerous females

Ovigerous *C. vagans* were caught in the Beagle Channel in September 2001 (54°53'S, 68°17'W, Fig. 1) using an inflatable dinghy equipped with an epibenthic

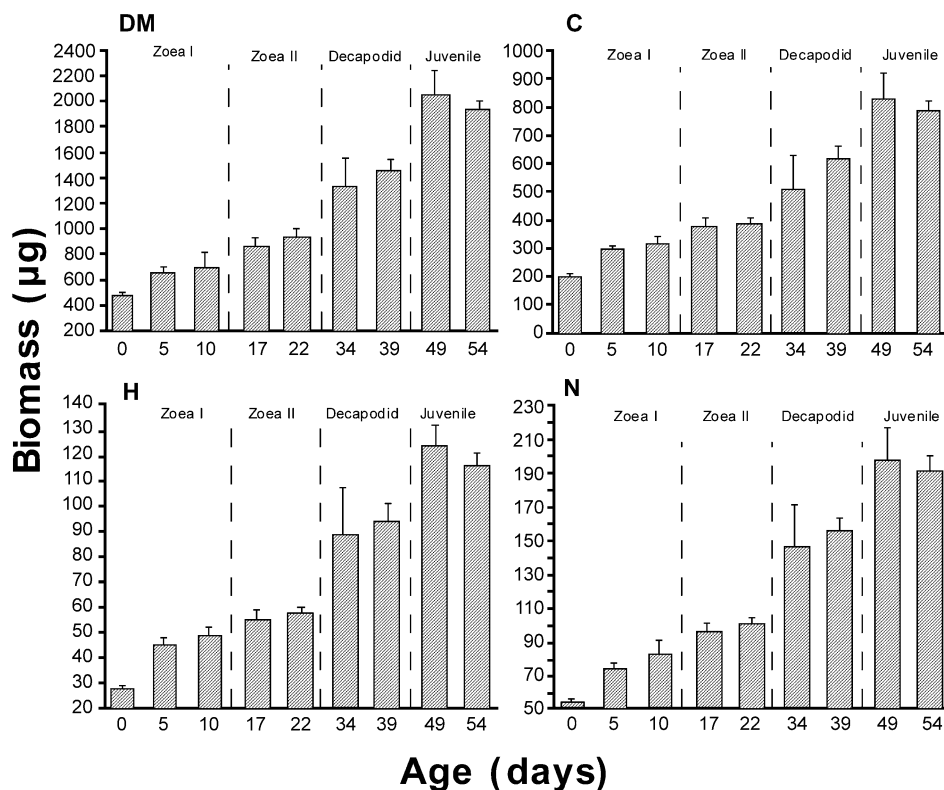


Fig. 1. *C. vagans*. Changes in dry mass (DM) and contents of carbon (C), nitrogen (N) and hydrogen (H) (all in µg/individual; $\bar{x} \pm S.D.$) during larval and early juvenile development in the presence of food (*Artemia* sp.).

trawl (1.7 m mouth width, net with 1 cm mesh size) at about 15 m depth. Maintenance of females and rearing of larvae took place in the local institute Centro Austral de Investigaciones Científicas (CADIC) in Ushuaia, Tierra del Fuego (Argentina), under constant conditions of temperature (7.0 ± 0.5 °C), salinity (ca. 30), and a 12:12-h light/dark rhythm.

Each female was kept individually in a tank of about 30 l water content, equipped with permanent seawater flow from a closed circulation filter system. Food (commercial TETRA AniMin pellets for aquaristics, TetraWerke, Germany) was given twice a week.

2.2. Rearing of larvae and juveniles

The first larvae hatched at night, about a fortnight after capturing the ovigerous females. Due to strong demersal behaviour, the larvae were collected every night from the bottom of the aquaria using long glass pipettes. Each day, randomly selected larvae were transferred to individual rearing cups with about 100 ml seawater, which were checked

daily for dead or moulted individuals. Every other day, water was changed and food (*Artemia* sp. nauplii; Argent Chemical Laboratories, USA) was supplied.

The larval development of *C. vagans* passed invariably through two zoeal stages and one decapodid stage, with mean durations of 12, 17 and 15 days, respectively (see Thatje et al., 2004). Their separation was based on the appearance of an exuvia and visual observation of morphological differences (cf. Thatje et al., 2001; Thatje and Lovrich, 2003).

2.3. Determination of dry mass (DM) and elemental composition (C, H, N)

Samples for the determination of dry mass (DM) and elemental composition (C, N, H; with $n=5$ replicates each; one individual per replicate) were taken immediately after hatching (day 0) and subsequently on days 5 and 10 of each larval and the first juvenile instar (see Table 1). Larval samples for the study of physiological changes during the complete larval and early juvenile development resulted from the same females A and B in parallel rearings. Due to extremely low fecundity (Thatje et al., 2004), parallel analyses of unfed larvae are based on larval material from an additional female. Exuviae were sampled from each larval stage to quantify biomass losses during successive moults. Since a minimum of 0.2 μg dry mass is needed for each elemental analysis, 10–20 exuviae (depending on availability) originating from two different females (females A+B) per replicate sample (with $n=1-6$ replicates) were pooled.

Dry mass was measured to the nearest 0.1 μg on an autobalance (Mettler, UMT 2). C, N and H contents of larvae and the first juvenile instar were analysed as described by Anger and Harms (1990): short rinsing in distilled water, blotting on fluff-free Kleenex paper for optical use, freezing at $-18\text{ }^{\circ}\text{C}$, vacuum drying at $<10^{-2}$ mbar,

Table 1

C. vagans. Changes in dry mass (DM) and contents of carbon (C), nitrogen (N) and hydrogen (H) (all in percent of DM; $x \pm \text{S.D.}$) during larval development and in the first juvenile shrimp stage in presence of food (*Artemia* sp.); age given in days (a) within each stage and (b) from hatching

Stage	Female	Age		DM ($\mu\text{g}/\text{individual}$) with <i>Artemia</i>		C (%DM) with <i>Artemia</i>		N (%DM) with <i>Artemia</i>		H (%DM) with <i>Artemia</i>	
		(a)	(b)	x	\pm	x	\pm	x	\pm	X	\pm
Zoea I	A	0	0	493	8	40.8	0.8	11.1	0.2	5.8	0.1
	B	0	0	426	55	43.5	5.0	11.8	1.5	6.2	0.7
	C	0	0	474	15	41.5	1.0	10.9	0.2	5.9	0.1
	D	0	0	416	36	42.4	0.6	11.7	0.3	6.2	0.1
	E	0	0	406	29	41.9	0.9	11.1	0.5	5.9	0.1
Zoea I	A	5	5	668	25	44.0	0.5	11.2	0.2	6.7	0.1
	A	10	10	712	77	44.0	0.5	11.6	0.3	6.7	0.1
Zoea II	A	5	17	903	51	40.7	1.7	10.7	0.4	6.0	0.3
	A	10	22	941	43	41.4	2.4	10.9	0.5	6.1	0.3
Decapodid	A	5	34	1342	221	44.2	1.5	10.9	0.1	6.5	0.3
	A	10	39	1446	49	44.3	1.6	10.8	0.3	6.6	0.3
Juvenile	A	5	49	2077	122	40.8	0.9	9.6	0.3	6.0	0.2
	A	10	54	1937	61	41.2	2.2	9.8	0.5	6.1	0.3

weighing and combusting at 1020 °C in a Fison (Carlo Erba) 1108 Elemental Analyser.

2.4. Protein analyses

Samples for protein analyses ($n = 5$) were gently rinsed in distilled water, dried on filter paper, transferred individually into an Eppendorf vial and deep frozen at -80 °C. Protein samples were dried for 48 h using the Finn-Aqua Lyovac GT2E vacuum drier, and W was afterwards measured in a Sartorius MC1 RC 210 S Balance (precision: 0,01 mg, capacity 210 g). Following drying, samples were homogenised by sonication (Branson, Sonifer, Cell Disruptor B 15) and each homogenate was divided in two aliquots for protein analyses. We used the Lowry method for protein determination (Lowry et al., 1951), modified to perform measurements using microplates (Pfaff, 1997, Paschke, 1998). Spectrometric measurements were made in triplicate in a microplate spectrophotometer (750-nm filter, Dynatech, MR 7000).

2.5. Total lipid and fatty acid analyses

Since the amount of larval material in all biochemical studies was extremely limited due to low female fecundity, we calculated individual total lipid content on the basis of lipid extraction, precipitation and drying, previous to transesterification of the sample material for fatty acid analyses.

The fatty acid composition was determined by gas chromatography (Kattner and Fricke, 1986). Briefly, fatty acids were converted to methyl esters by transesterification in methanol containing 3% concentrated sulphuric acid at 80 °C for 4 h. The obtained fatty acid methyl esters were then analysed using a gas chromatograph (GC) (HP6890) on a 30 m \times 0.25 mm i.d. wall-coated open tubular column (film thickness: 0.25 μ m; liquid phase: DB-FFAP) using temperature programming. Fatty acids were identified with standard mixtures and quantified by internal standard (Kattner et al., 1998).

2.6. Statistical analyses

Differences in larval elemental composition at hatching were compared in five different females. Statistical differences were tested by means of a one-way ANOVA

Table 2

C. vagans. Changes in dry mass (DM) and contents of carbon (C), nitrogen (N) and hydrogen (H) (all in percent of DM; $x \pm$ S.D.) in the zoea I stage in the absence of food; age given in days

Stage	Female	Age	DM (μ g/individual) without <i>Artemia</i>		C (%DM) without <i>Artemia</i>		N (%DM) without <i>Artemia</i>		H (%DM) without <i>Artemia</i>	
			x	\pm	x	\pm	x	\pm	x	\pm
Zoea I	C	0	474	15	41.5	1.0	10.9	0.2	5.9	0.1
	C	5	455	23	37.7	1.0	10.6	0.3	5.5	0.1
	C	10	441	16	37.5	1.1	10.4	0.3	5.3	0.2

(Sokal and Rohlf, 1995). Changes in dry mass, elemental composition (C, N, H), protein and lipid were described and compared with linear regressions in relation to larval age (Sokal and Rohlf, 1995). The elemental and protein data were log-transformed to achieve normality and homoscedasticity (tested with Kolmogorov–Smirnov and Bartlett’s tests, respectively). Slopes of linear regressions were compared with an ANCOVA using the F -statistic (Sokal and Rohlf, 1995).

3. Results

3.1. Changes in dry mass, C, N, H and C:N mass ratio

The elemental composition and protein content of recently hatched larvae varied significantly among the five different females (DM, $F=6.753$, C, $F=10.787$, H, $F=13.218$, N, $F=10.707$, proteins $F=16.2$; all $P<0.001$).

First feeding was microscopically observed following hatching. Dry mass as well as C, H and N increased significantly in fed larvae from hatching to metamorphosis, reaching fourfold higher values on day 5 of the first juvenile stage (Tables 1 and 3; Fig. 1). A stronger increase in the C fraction in relation to DM is reflected by an increasing C:N mass ratio during larval development. This ratio remained comparably constant from day 5 to day 22 (end of zoea II stage), but increased subsequently from about 3.8 to 4.1, when the decapodid stage was reached (Fig. 2).

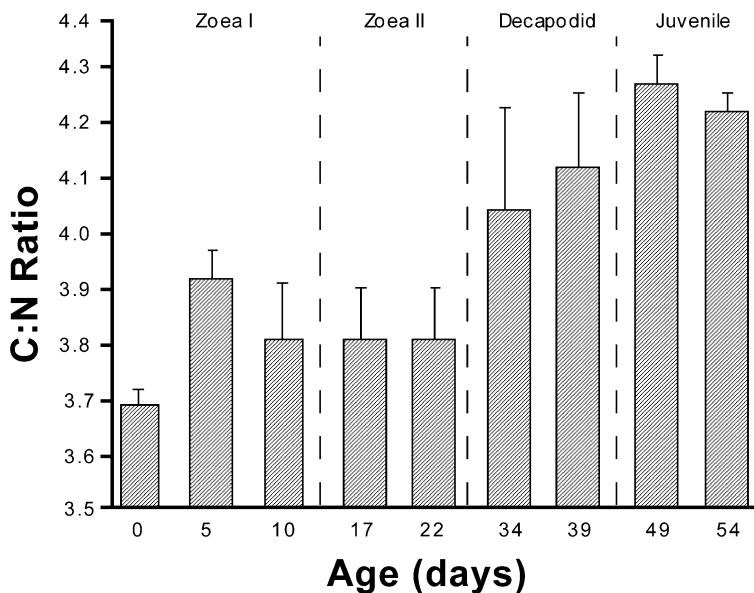


Fig. 2. *C. vagans*. Carbon/nitrogen (C:N) mass ratio during larval and early juvenile development in the presence of food (*Artemia* sp.).

Table 3

C. vagans. Parameters of linear regressions describing changes in dry mass (DM), contents of carbon (C), nitrogen (N), hydrogen (H) (all in $\mu\text{g}/\text{individual}$, after logarithmic transformation) as functions of the time of development during larval development until day 5 of the first juvenile instar (i.e. day 49 of development)

Stage	Biomass parameter	Slope	Intercept	F reg	P
<i>With Artemia</i>					
Zoea I–Decapodid (days 0–49)	DM	0.012	2.735	925.0	<0.001
	C	0.012	2.362	627.5	<0.001
	H	0.012	1.533	466.2	<0.001
	N	0.011	1.790	774.5	<0.001
	Proteins	0.010	2.367	148.7	<0.001
<i>Without Artemia</i>					
Zoea I (days 0–10)	DM	–0.003	2.676	9.76	0.008
	C	–0.008	2.290	52.45	<0.001
	H	–0.008	1.448	41.09	<0.001
	N	–0.005	1.714	28.98	<0.001
	Proteins	–0.008	2.365	1.951	0.186

All slopes are significantly different from zero ($P < 0.001$); the slopes of regressions obtained from different treatments do not differ significantly from each other (ANCOVA: all $P > 0.05$).

Despite the significant differences in elemental composition and protein content of recently hatched larvae among all five females, the initial elemental composition and protein contents of larvae from female A (with *Artemia*) and female C (without *Artemia*) were similar (Tukey post hoc tests for C, N, H and protein per larvae, all $P > 0.41$; Tables 1–3). Larvae kept under starvation conditions (female C) did not reach the moult to the zoea II stage. DM, C, N and H decreased significantly within the first 10 days of the zoea I (Table 3), when this sampling was finished due to lack of larval material. The protein content, in contrast, remained constant throughout this time span (cf. Table 2). Starved larvae survived on average about 14 days. In fed larvae, the proportion of C, N and H (in %DM) remained equal during the entire larval and early juvenile development (Table 1). C contributed always about 40–44%

Table 4

C. vagans. Dry mass (DM), contents of carbon (C), nitrogen (N) and hydrogen (H) (all in $\mu\text{g}/\text{individual}$ and in percent of W), C:N mass ratio of the exuviae of all larval stages; $\bar{x} \pm \text{S.D.}$

Stage		N	DM		C		N		H		C:N mass ratio	
			\bar{x}	\pm	\bar{x}	\pm	\bar{x}	\pm	\bar{x}	\pm	\bar{x}	\pm
Zoea I	$\mu\text{g}/\text{ind.}$	7	39.3	4.2	7.4	1.3	1.3	0.1	1.2	0.2	5.6	1.1
	%DM		8.5	0.9	1.6	0.2	0.3	0.1	0.3	0.1		
Zoea II	$\mu\text{g}/\text{ind.}$	5	57.8	13.1	10.2	1.0	1.9	0.2	1.6	0.2	5.3	0.1
	%DM		12.4	2.9	2.2	0.2	0.4	0.1	0.3	0.1		
Decapodid	$\mu\text{g}/\text{ind.}$	1	74.9		16.4		3.2		2.7		5.2	
	%DM		16.3		3.6		0.7		0.6			

DM, while the N and H values ranged from about 10–12% and 6–7%, respectively (Table 1). The values for unfed larvae of female C were slightly below those of fed larvae (Table 1).

3.2. Exuvial losses

Very few exuviae were available for elemental analyses, especially in late developmental stages, hence no replicate analyses were possible (Table 4); many exuviae fell rapidly apart shortly after moulting.

The zoeal stages as well as the decapodid stage of *C. vagans* produced strikingly thin and fragile exuviae. Therefore, total exuvial dry mass and C, N, H contents per individual were low, but gradually increased in successive ontogenetic stages, more or less doubling the above values of zoea I exuviation at metamorphosis (Table 3; Fig. 3). The C, N, H values (in percent of exuvial DM) were generally much lower than those of the whole body mass. The C:N mass ratio, in contrast, was always higher in the exuviae than in total body DM of larval and juvenile stages (Tables 1 and 4).

In both zoeal stages combined, about 21% of the initial DM at hatching, 4% of the initially present C, and about 1% of both, N and H was lost with the shed exuviae. Roughly the same amounts were lost with the decapodid exuvia cast at metamorphosis. The losses in DM, however, were slightly lower in the decapodid, compared to those in the zoeal stages I and II combined (Fig. 3). Total exuvial losses of DM from hatching to metamorphosis (all larval stages combined) amounted to about 172 μg DM or 37% of the initially present dry mass at hatching (Fig. 3).

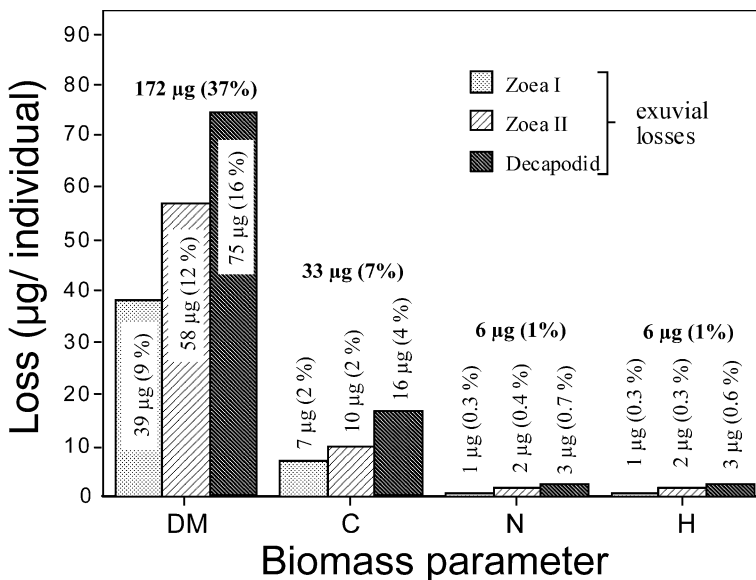


Fig. 3. *C. vagans*. Exuvial losses of dry mass (DM), carbon (C), nitrogen (N) and hydrogen (H), given in μg /individual ($x \pm \text{S.D.}$) and in percent of the initial biomass at hatching.

Table 5
Changes in the protein content ($\mu\text{g}/\text{individual}$) during larval and early juvenile development of *C. vagans* (– *Artemia* = without *Artemia* sp.)

Female		Developmental stage							
		Zoea I			Zoea II		Decapodid		Juvenile I
		d-0	d-5	d-10	d-17	d-22	d-34	d-39	d-49
A	$\mu\text{g}/\text{ind.}$	189.5 \pm 30.7	281.3 \pm 25.2	336.1 \pm 37.8	388.1 \pm 38.6	389.5 \pm 49.1	496.1 \pm 46.8	587.4 \pm 65.6	642.1 \pm 204.8
	%DM	38.6 \pm 0.7	42.1 \pm 1.6	47.5 \pm 5.8	43.1 \pm 2.5	41.4 \pm 1.9	37.8 \pm 6.5	40.6 \pm 1.4	31.0 \pm 1.7
B	$\mu\text{g}/\text{ind.}$	201.1 \pm 21.1	280.8 \pm 68.6	273.0 \pm 34.3	326.5 \pm 38.5	407.6 \pm 56.9	479.4 \pm 39.4		
	%DM	48.0 \pm 6.6	46.5 \pm 6.6	40.9 \pm 1.6	35.9 \pm 2.6	44.2 \pm 5.1	37.4 \pm 1.9		
C – <i>Artemia</i>	$\mu\text{g}/\text{ind.}$	229.6 \pm 77.6	236.5 \pm 12.0	181.1 \pm 11.9					
	%DM	48.3 \pm 1.5	51.9 \pm 2.5	63.9 \pm 2.2					
D	$\mu\text{g}/\text{ind.}$	209.3 \pm 18.6							
	%DM	49.8 \pm 6.9							
E	$\mu\text{g}/\text{ind.}$	191.1 \pm 27.6							
	%DM	47.2 \pm 3.6							

d-0: freshly hatched larvae (unfed).

3.3. Changes in protein and lipid contents

The protein content varied from 31% to 50% of DM (Table 5). The gradual increase in the absolute protein content (in $\mu\text{g}/\text{individual}$) during larval development showed a similar pattern as observed in elemental composition. Larvae maintained without food lost about 22% from hatching to day 10, indicating significant protein utilisation.

Total lipid content increased continuously from hatching to the first juvenile instar (37–95 $\mu\text{g}/\text{individual}$, Table 6), however, with variable values in the decapodid stage (Table 6). In terms of %DM, lipid contents of about 8% decreased slightly throughout larval development (Table 6). A decreasing lipid content by about 27% in the decapodid stage a few days before metamorphosis (from day 34 to day 39) indicates a considerable use of lipids (Table 6). Total lipid in larvae kept under starvation conditions decreased from hatching until day 5. This may indicate utilisation of lipids as an energy source during absence of food (Table 6).

3.4. Fatty acid composition

The dominant fatty acids during the subsequent larval development of *C. vagans* were 18:1(n-9), 16:0 and 20:5(n-3), contributing on average 20%, 15% and 12%, respectively, to the total fatty acid pool (Table 7). Other important fatty acids were 18:1(n-7), 18:3(n-3), 18:0 and 16:1(n-7), contributing 8%, 7%, 6% and 4%, respectively, to the total fatty acid pool (Table 7). Other fatty acids occurred only in small amounts and most of these were polyunsaturates. On average, about 15% saturated, 35% monounsaturated and 40% polyunsaturated fatty acids were found throughout larval and early juvenile development (Table 7).

The food offered (*Artemia* sp. nauplii) was dominated by 18:1(n-9), 18:3(n-3), 16:0 and 16:1(n-7), contributing 29%, 22%, 12% and 6%, respectively, to all fatty acids (Table 7). The strong variability in fatty acid content as, e.g. observed throughout larval development in 18:3(n-3), might be due to individual feeding conditions of larvae (Table 7). After 10 days of starvation, a dramatic decrease occurred in all previously dominating fatty acids (all < 7%).

The contribution of three detected fatty alcohols (14:OA, 16:OA, 18:OA) was extremely low in all samples; they varied from 0 to 3% of total mass, indicating

Table 6

C. vagans. Total lipid content in fed and unfed (– *Artemia* = without *Artemia*) larvae (all in $\mu\text{g}/\text{individual}$ and in percent of DM)

Female	Developmental stage	Zoea I			Zoea II		Decapodid		Juvenile I	
		d-0	d-5	d-10	d-17	d-22	d-34	d-39	d-49	d-54
		A	$\mu\text{g}/\text{ind.}$	37	52	64	60	63	51	37
	%DM	8	8	9	7	7	4	3	5	4
C – <i>Artemia</i>	$\mu\text{g}/\text{ind.}$	41	11	39						
	%DM	9	2	9						

Table 7

C. vagans. Changes in fatty acid composition (mass percent of total fatty acids) during larval and early juvenile development, and in the *Artemia* nauplii offered as food

Fatty acids	Zoea I			Zoea II		Decapodid		Juvenile I		<i>Artemia</i> sp.
	d-0	d-5	d-10	d-17	d-22	d-34	d-39	d-49	d-54	
13:0	0.4	0.3	0.2	0.2	0.4	0.1	–	–	–	–
14:0	3.0	2.1	1.8	2.3	2.8	1.1	0.9	7.0	1.3	1.0
14:1(n-5)	0.4	0.2	–	–	–	–	–	–	–	0.1
15:0	1.2	0.7	0.4	1.3	1.5	0.3	0.3	0.4	0.3	0.4
16:0	18.8	13.9	13.8	16.3	15.5	13.9	11.4	17.3	11.6	11.7
16:1(n-7)	3.3	3.8	3.8	3.7	3.7	4.3	4.2	9.3	3.8	6.1
16:1(n-5)	0.3	0.2	–	0.3	–	0.1	0.1	0.2	0.1	0.2
16:2(n-4)	0.7	0.4	0.5	0.4	0.3	0.2	0.2	1.9	–	0.3
16:3(n-4)	0.8	0.9	0.9	1.0	1.2	1.0	0.9	1.6	0.9	1.2
16:4(n-1)	0.5	–	–	0.2	–	–	0.2	3.1	0.8	–
17:0	1.1	0.7	0.7	1.0	1.6	0.9	0.7	0.3	0.7	0.7
17:1	–	0.1	–	0.3	–	0.2	0.2	–	–	0.6
18:0	7.4	7.1	5.8	6.8	7.8	6.1	5.3	2.9	5.9	3.5
18:1(n-9)	12.9	19.9	20.8	20.5	21.5	25.7	24.6	12.2	24.7	29.2
18:1(n-7)	7.5	8.2	8.8	7.8	8.1	12.3	10.7	2.5	10.1	7.1
18:2(n-6)	2.6	9.4	4.6	6.6	5.8	5.9	4.7	0.9	4.9	5.1
18:3(n-6)	0.7	0.6	1.0	0.7	0.4	2.1	0.8	0.4	1.4	1.3
18:3(n-3)	0.4	0.3	10.9	11.1	5.3	0.4	15.5	0.7	14.4	21.5
18:4(n-3)	–	0.8	0.9	1.1	1.0	1.6	1.5	3.4	1.3	4.1
20:1(n-9)	0.5	0.5	0.9	1.0	1.1	1.3	1.2	1.2	1.1	0.7
20:1(n-7)	0.7	0.5	0.3	0.2	–	0.3	0.3	0.2	–	–
20:2(n-6)	0.4	2.3	–	0.1	0.6	0.5	0.4	–	–	–
20:3(n-6)	0.5	0.3	–	0.2	0.3	0.1	0.2	0.2	–	0.2
20:3(n-3)	–	0.3	0.4	0.4	3.5	1.0	0.8	1.1	0.9	0.2
20:4(n-6)	3.6	3.0	2.9	2.0	1.6	3.1	2.8	0.7	2.7	1.0
20:4(n-3)	–	0.3	–	0.3	–	0.5	0.4	–	–	0.3
20:5(n-3)	16.3	12.7	11.7	8.6	8.7	11.3	8.1	19.7	9.9	3.5
22:1(n-11)	–	–	–	–	–	–	–	1.8	–	–
22:1(n-9)	0.4	0.2	–	0.4	–	0.2	0.1	0.2	–	–
22:4(n-3)	2.5	1.3	1.1	1.0	1.2	0.6	0.5	0.8	0.7	–
22:5(n-3)	1.1	0.6	0.4	0.8	0.3	0.2	–	1.3	–	–
22:6(n-3)	12.1	8.4	7.3	3.6	5.8	4.4	2.8	8.5	3.5	–
24:1(n-11)	–	–	–	–	–	–	–	0.4	–	–
Σ Saturates	31.8	24.7	22.8	27.7	29.6	22.4	18.7	28.0	19.7	17.3
Σ Monounsats.	26.0	33.7	34.6	34.2	34.4	44.4	41.4	27.9	39.8	44.1
Σ Polyunsats.	42.2	41.6	42.6	38.1	36.0	33.2	39.9	44.1	40.5	38.6

that wax esters were negligible as an energy source during starvation and metamorphosis.

4. Discussion

Based on the comprehensive work of Thorson (1936, 1950), it has been suggested that polar marine invertebrates tend to reduce planktotrophic larval developments

(Mileikovsky, 1971). This generalisation generated intense scientific discussions and was frequently modified (e.g. Chia, 1974; Stanwell-Smith et al., 1999; Gallardo and Penchaszadeh, 2001; see also Arntz and Gili, 2001). At high latitudes, there exists a conspicuous mismatch of long larval development due to low temperatures and short intensified periods of primary production, i.e. food availability (Clarke, 1982, 1987). This should select against a planktotrophic mode of development, in particular in the high Antarctic regime. Studies on invertebrate reproduction in the Southern Ocean demonstrated that reproductive traits in cold environments are more diverse than previously assumed. This includes a high frequency of brooding species including those with benthic, demersal or direct larval development (Bosch and Pearse, 1990), which is often associated with various levels of food independence. Pelagic studies showed that the meroplanktonic community may be more diverse than previously recorded, occurring in low abundance, but with long-lived and slowly developing larvae (Stanwell-Smith et al., 1999). Such modes, however, require some degree of endotrophic or partially lecithotrophic development allowing for a high resistance to starvation. These processes are still far from understood in high latitudinal benthic decapods.

In the subantarctic Magellan region, the meroplanktonic community is dominated by decapod larvae (Lovrich, 1999; Thatje et al., 2003b). For instance, endotrophic food-independent, demersal modes of development have been observed in some lithodid crabs (e.g. Calcagno et al., 2003; Lovrich et al., 2003), but planktotrophic or partially food-independent developments seem to be the dominating modes in decapod reproduction (Thatje et al., 2003b). The use of plankton as a food source basically requires a strong synchronisation of larval release with seasonal peaks of plankton productivity. Such hatching processes may be triggered by sinking phytoplankton particles to the sea floor, or directly by the development of a phytoplankton bloom (Starr et al., 1990, 1994). On the other hand, some decapods at high latitudes show extended hatching periods of varying length, ranging from a few weeks to months (e.g. Lithodidae: *Paralomis granulosa*, *Lithodes santolla*, Thatje et al., 2003a; Crangonidae: *Notocrangon antarcticus*, Bruns, 1992). This same pattern is evident also in *C. vagans* with 2–3 weeks of duration (Thatje et al., 2004). Extended periods of larval release in combination with high larval resistance to starvation (for *C. vagans*, see Thatje et al., 2004) reduce the necessity of synchronisation with food availability (Stanwell-Smith et al., 1999). In addition, low daily hatching rates should help to avoid predation on the small offspring (Thatje et al., 2003a). Extended hatching periods occur also in decapod species with completely food-independent larvae (e.g. the lithodid *P. granulosa*; Calcagno et al., 2003). The abbreviated larval development in *C. vagans* may be another important adaptation to food limitation, as it allows a better synchronisation with food availability. Lack of variability in the number of instars appears to be typical of high latitudinal caridean species, again aiding to synchronisation with peaks in plankton production (high variability in larval developmental pathways is typical of low latitude decapods, i.e. tropic carideans, Wehrtmann and Albornoz, 1998; Anger, 2001). The production of extremely thin exuviae in *C. vagans* is an energy saving mechanism (Anger, 2001). This was demonstrated also in lithodid crab larvae from cold-temperate regions (e.g. Lovrich et al., 2003).

Most campylonotid species (*C. vagans*, *C. semistriatus*, *C. rathbunae*) apparently have an abbreviated larval development (Thatje et al., 2001). Larvae of these species usually occur in extremely low abundance in the plankton, which is typical of high latitudinal meroplankton communities (Stanwell Smith et al., 1999; Thatje et al., 2003b). Since also larvae of the deepwater species *C. capensis* migrate vertically to the upper ocean stratum (larvae have been found from 100 m depth to sea surface, Thatje et al., 2001), a planktotrophic and abbreviated larval development may be typical of this family. Although larvae of *C. vagans* showed a carnivorous feeding behaviour, they may actually be omnivorous. Nutritional dependence on secondary production (mesozooplankton) would explain an extended mode of hatching, since the development of a phytoplankton bloom would only predict subsequent food availability in developing zooplankton. However, Bruns (1992) assumed that the extended hatching mode in a high Antarctic herbivorous caridean, *N. antarcticus*, may represent a mechanism of synchronisation with primary production which, in the case of the high Antarctic shelf, is highly variable due to annual variability in the sea ice extent (Strass and Fahrbach, 1998). Recently, Graeve and Wehrtmann (2003) demonstrated that eggs of polar crustaceans do not contain significantly more lipids than species from tropical regions (see also Wehrtmann and Kattner, 1998). This was surprising, because previous studies suggested that high latitudinal crustacean eggs, which are generally larger, have a higher nutrient content per embryo (Clarke, 1993), as the adult Antarctic shrimps appear to accumulate large amounts of lipids (Clarke, 1983, 1987). Larger eggs are assumed to reflect environmental conditions such as low temperature, often associated with hatching of advanced larvae and an abbreviated development (for discussion, see Clarke, 1993; Wehrtmann and Kattner, 1998; Anger et al., 2002). Total lipid contents of *C. vagans* larvae are low, but in the usual range of carideans from temperate zones (Graeve and Wehrtmann, 2003). Starved larvae rely mainly on proteins as internal energetic contents. The dominating fatty acids utilised during the course of larval development are very similar to the fatty acids found in eggs of Antarctic shrimps (Graeve and Wehrtmann, 2003). The variability in the fatty acid composition during the larval development in *C. vagans* is high (Table 7). This may be due to intraspecific variability in larval fitness and feeding condition. Especially the fatty acid 18:3(n-3) which resulted mainly from food uptake (Table 7) may indicate feeding conditions of larvae. Other dominant fatty acids remained comparably constant during the complete larval development (Table 7). Larval starvation is especially known before ecdysis (Anger, 2001) and the fatty acid composition should help to distinguish periods of active feeding from starvation. However, since our samples were always taken at days 5 and 10 of each stage, but subsequent larval stages are of different length in duration (Thatje et al., 2004, zoea I: 12, zoea II: 17, decapodid: 15 days in duration), we need a higher temporal dissolution in future sampling.

In conclusion, the present observations of planktotrophic development in a caridean shrimp from the cold-temperate Magellan region suggests that actively feeding decapod larvae with a high starvation resistance, in combination with a strongly abbreviated mode of larval development, is a successful reproductive strategy at higher latitudes.

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