Reproductive trade-offs in benthic decapod crustaceans of high southern latitudes: tolerance of cold and food limitation

Reproduktionsstrategien benthischer Zehnfußkrebse hoher südlicher Breitengrade: Toleranz von Kälte und Nahrungsmangel

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Berichte zur Polar- und Meeresforschung, Nr. 483
Reports on Polar and Marine Research, No. 483
ISSN 1618 - 3193

The most beautiful thing we can experience is the mysterious.

It is the source of all true art and science.

Albert Einstein

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Die vorliegende Arbeit ist die kaum veränderte Fassung einer kumulativen Dissertation, die in der Sektion "Vergleichende Ökosystemforschung" bei Prof. Dr. Wolf E. Arntz angefertigt und dem Fachbereich 2 (Biologie/Chemie) der Universität Bremen im April 2003 vorgelegt wurde.

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SUMMARY

Caridean shrimps comprise the only decapod infraorder in the markedly impoverished high Antarctic decapod fauna. Their presence, with about a dozen species only, was previously assigned to their capability of down-regulating high haemolymph magnesium ($[Mg^{2+}]_{HL}$) concentrations at low temperatures. This regulation is missing or insufficient in reptant decapods, affecting in particular their scope of activity. This deficiency has been hypothesised as one important factor explaining their extinction during Antarctic cooling in the Tertiary, as evidenced by the fossil record.

The present work demonstrates an ecological adaptation in the early life history of decapods to ecophysiological constraints in the cold, primarily a mismatch between reproductive traits and a marked seasonality of primary production and low temperatures increasing with latitude. It is shown that on a macroecological scale, natant decapods show remarkable plasticity in changing their early life history patterns with latitude and decreasing water temperature. These changes include, for example, an increase in egg size, hatching of large and advanced larvae and a reduction of fecundity with latitude. Energy saving traits to abbreviate larval developments such as a strong suppression of the number of instars, low metabolic losses in very thin exuviae during fewer moults, and a loss of highly variable developmental pathways compared to lower latitides, are observed already in the Subantarctic realm of southernmost America. Early larvae generally present a high resistance to starvation, which in combination with an abbreviated larval development allows for a better synchronisation with peaks in food availability. However, caridean larvae rely on primary production, and the evolutionary step towards complete endotrophic larval development, possibly due to phylogenetic constraint, is almost unknown in marine shrimps.

The need for food in planktotrophic and extended larval development of ancestor reptants, and the lacking resistance of larvae to starvation as well as their low tendency of suppressing the number of larval instars, is herein supposed to have selected against Reptantia at high latitudes. However, it is shown that lithodid crabs, which evolved fairly recently about 13 to 25 Ma ago, did develop early life history adaptations to cold environments. Two lithodid crab species from the Subantarctic Magellan region (*Lithodes santolla*, *Paralomis granulosa*) developed complete food independent lecithotrophic and strongly abbreviated development of demersally living larvae, and a high tolerance to low temperatures typical of the Antarctic. Under present climate conditions, these anomuran crabs may represent a reptant group that might be able to recuperate the polar environments as a habitat for reptants, as already indicated by a few recent records of lithodids off the Antarctic continental shelf.

ZUSAMMENFASSUNG

Caridea sind die einzigen Vertreter der artenarmen hochantarktischen Decapodenfauna. Ihre Präsenz mit nur etwa 12 Arten wurde ihrer Fähigkeit zugesprochen, Magnesiumkonzentrationen in der Hämolymphe ($[Mg^{2+}]_{HL}$) bei niedrigen Temperaturen herabregulieren zu können. Diese Regulationsfähigkeit fehlt oder ist nur gering ausgebildet in den reptanten decapoden Krebsen, wodurch ihre Aktivität stark reduziert wird. Das Fehlen der Magnesiumregulierung wurde als möglicher Faktor für die Auslöschung reptanter Krebse während der Abkühlungsprozesse der Antarktis im Tertiär hypothetisiert. Die Auslöschung der Reptantia während dieses Zeitraums wurde durch Fossilienfunde belegt.

Diese Arbeit befasst sich mit den Prozessen ökologischer Anpassung früher Lebensstadien (Embryonen und Larven) decapoder Krebse an ökophysiologische Zwänge unter Kältebedingungen. Diese ökophysiologische Zwänge basieren insbesondere auf einem Ungleichgewicht zwischen Reproduktionszyklen und einer kurzen und stark saisonalen Primärprodukion, kombiniert mit niedrigen Temperaturen, und nimmt mit geographischer Breite zu. Aus makroökologischer Sicht zeigen natante Garnelen (Caridea) eine bemerkenswerte Plastizität in ihren frühen Lebensstadien als Konsequenz zu den mit steigendem Breitengrad abnehmenden Wassertemperaturen. Beispiele dieser Anpassung sind ein stetiges Grössenwachstum der Eier, grössere und in ihrer Entwicklung weiter vorangeschrittene Larven zum Zeitpunkt des Schlupfes, sowie eine geringere Fekundität mit steigendem Breitengrad. Bereits in der Subantarktis des südlichen Amerika konnten im Vergleich zu niedrigeren Breiten Energie einsparende Eigenschaften in Richtung einer stark abgekürzten Larvalentwicklung, geringere metabolische Verluste in sehr dünnen Exuvien und einer geringeren Anzahl an Häutungen, sowie der Verlust der Variabilität in larvalen Entwicklungszyklen, beobachtet werden. Frühe Larven zeigen eine hohe Hungerfähigkeit, welche in Kombination mit einer abgekürzten Larvalentwicklung zu einer besser Synchronisierung mit Höhepunkten in der Nahrungsverfügbarkeit führt. Trotzdem sind die Caridea abhängig von Primärproduktion. Der evolutionäre Schritt in Richtung komplett endotropher Larvalentwicklung ist kaum bekannt und vermutlich durch phylogenetische Zwänge bedingt.

Die Notwendigkeit planktotropher Nahrung und eine verlängerte Larvalentwicklung der verwandten reptanten Decapoda, sowie die mangelnde Fähigkeit ihrer Larven zu hungern und auch eine abgekürzte Larvalentwicklung zu durchlaufen, wird hiermit als ein Selektionsmechanismus gegen die Reptantia in hohen Breitengraden angenommen. Im Gegensatz dazu haben die lithodiden Krebse, die sich erst vor etwa 13 bis 25 Mio. Jahren entwickelt haben, frühe Lebensstadien entwickelt, die eine Anpassung an Kälte aufweisen. Zwei Arten der Lithodidae aus der subantarktischen

Magellanregion (*Lithodes santolla*, *Paralomis granulosa*) haben eine komplett nahrungsunabhängige lecithotrophe und stark abgekürzte Larvalentwicklung in demersalen Larven hervorgebracht, und weisen zudem eine hohe Toleranz gegenüber niedrigen und antarktistypischen Temperaturen auf. Unter gegebenen Klimaverhältnissen könnten die Lithodiden eine reptante Decapodengruppe darstellen, die in der Lage ist die Polargebiete wieder zu besiedeln. Einige wenige rezente Funde lithodider Krebse unterhalb des antarktischen Schelfs unterstützen diese Annahme.

1 INTRODUCTION

1.1 DECAPOD CRUSTACEANS IN POLAR AREAS

With over 42,000 species described so far, decapods represent one of the largest taxa in the animal kingdom, only outnumbered by insects and gastropods (Bowman and Abele, 1982; Tudge, 2000). Almost 90 % of all decapod species live in the oceans or adjacent brackish water, and at least 1000 species were able to colonise limnic habitats (Kaestner, 1980). Although in much lower numbers (< 100 species), in the course of their evolution decapods were also able to conquer firm land (Hartnoll, 1988). Most decapods are benthic, living at the seafloors of oceans, rivers and lakes, and their life history is rather complex (Anger, 2001). Instead of developing directly from the egg to a benthic juvenile stage, most species produce pelagic larvae and these pelagic stages had to adapt to an environment, which is rather variable and different from that of the adult conspecifics. Therefore, decapod larvae had to adapt to more variable selective forces in the pelagic than their benthic parents, such as temperature, salinity, and/or food availability, and have evolved their own evolutionary adaptations, principally in morphology, locomotion and physiology (Williamson, 1982; Anger, 2001; Anger, 2003).

The low number of decapod species found in the polar marine realm of both hemispheres is quite remarkable, when compared to other seas. In the Southern Ocean, only about twelve benthic caridean shrimps have been found hitherto on the Antarctic continental shelf and the adjacent deep sea (Yaldwyn, 1965; Maxwell, 1977; Gorny, 1999), and only about 5 species live on the high-Antarctic Weddell Sea shelf (Arntz et al. 1992). Except for some lithodid crabs that have recently been found in the Antarctic Bellingshausen Sea (Klages et al., 1995; Arana and Retamal, 2000), reptants are not known from high polar areas, where water temperature at the seafloor drops permanently below about 0°C. Although distribution patterns in decapod diversity in high southern latitudes should be greatly impacted by the Antarctic Circumpolar Current (ACC) and the deep sea, both surrounding and isolating the Antarctic marine realm, the diversity pattern in decapod crustaceans should principally be the same in the Arctic. Due to geographic connections of the Arctic with adjacent sub-Arctic and boreal re-

gions, however, the pattern of decapod biogeography is not as clear as in the Southern Ocean. Carideans also dominate the high Arctic regime (Squires, 1966; 1990), but temperatures at the seafloor of the Bering Sea, where various commercially exploited reptant species such as *Chinoecetes opilio* and *Paralithodes camtschatica* occur in great abundance, are higher with averages between –1 and +1 °C, or even higher annual means (Mallet et al., 1993; annual mean from 1983 to 1993: +3.4 °C, see Stevens et al., 1996).

1.2 SYSTEMATICS AND SPECIES STUDIED

A systematic division of the Decapoda into the suborders Reptantia and Natantia was introduced by Boas (1880) and Borradaile (1907). Recently, Kästner (1993) preferred the division into the suborders Dendrobranchiata (infraorder Penaeidae) and Pleocyemata (infraorders Stenopodidea, Caridea, Astacidea, Thalassinidea, Palinura, Anomura, and Brachyura), thus dissolving the suborders Reptantia and Natantia. Kästner's classification (1993) considers the Natantia to be paraphyletic (Abele, 1991; Scholz and Richter, 1995), but does not consider the Reptantia as a true monophyletic group (Scholz and Richter, 1995). As the systematics of the Decapoda is still subject to controversial discussion, the present work is based on the division into Reptantia and Natantia, which in addition facilitates the outline of the problem of low decapod diversity in high latitudes.

Along the Pacific coast off South America, the hippolytid shrimp *Nauticaris magellanica* (A. Milne Edwards, 1891, Fig. 1A) is known to occur over approximately 35 degrees of latitude, thus being an ideal species for the comparison of life history adaptations to changing environmental conditions, mainly temperature, with latitude (Wehrtmann and Kattner, 1998; Thatje and Bacardit, 2000c). *Nauticaris magellanica* is occurring in shallow subtidal habitats, and is an abundant species associated with mussel raft cultures and holdfasts of the kelp *Macrocystis porifera* (Aracena and López, 1973; Ojeda and Santelices, 1984). At the Atlantic coast of South America, this species is distributed from the coastal waters off Buenos Aires (Argentina) south to the Magellan region and the Falkland Islands (Boschi et al., 1992; Spivak, 1997).

Members of the genus *Campylonotus*, which forms the monogeneric caridean family Campylonotidae Sollaud, 1913, represent shallow-water to deep-sea species predominantly living in Subantarctic regions (Thatje et al., 2001; Thatje, 2003). This genus has a circumpolar distribution (Spivak, 1997; Yaldwyn, 1960), and its first representative from Antarctic waters, *Campylonotus arntzianus* (Thatje, 2003; Fig. 1B), is described herein. The biogeographic restriction of the Campylonotidae to the Southern Ocean suggests that the evolution of life history adaptation in this caridean family and the history of the Southern Ocean are strongly linked.

The two lithodid anomurans studied in this thesis, *Paralomis granulosa* (Jaquinot) and *Lithodes santolla* (Molina), are a characteristic faunistic element of the decapod fauna in the subantarctic Magellan region of South America, and constitute an important target of the local artisanal trap fishery in both southern Chile and Argentina (Campodonico, 1971; Lovrich, 1997). *Lithodes santolla* (Fig. 1C) and *P. granulosa* (Fig. 1D) show a bathymetric distribution from the shallow sublittoral to approximately 700 m and 300 m water depth, respectively (Boschi et al., 1992).

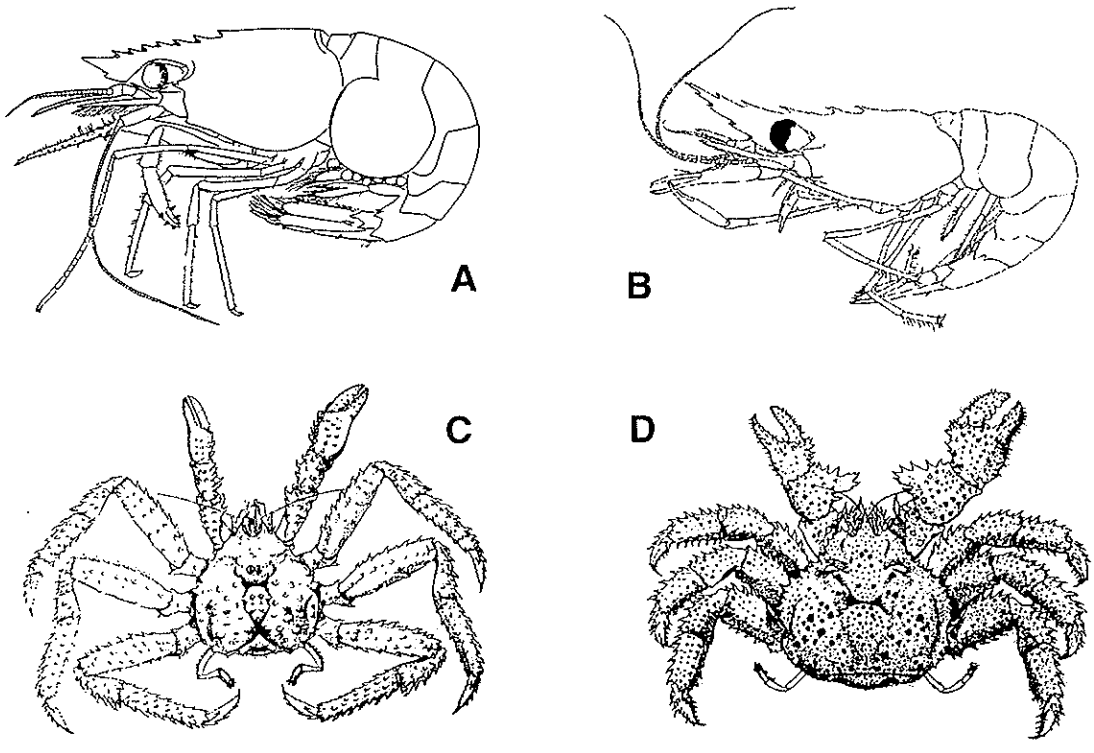


Fig. 1. Species studied in the present thesis; A: *Nauticaris magellanica*; B: *Campylonotus arntzianus*; C: *Lithodes santolla*; D: *Paralomis granulosa*; A, C-D, changed after Boschi et al., 1992; B, changed after Thatje, 2003.

1.3 PHYSIOLOGICAL BACKGROUND

Low temperature is the main physiological impact to life in polar areas, and is causing low metabolic rates in polar ectotherms (Clarke, 1983; Peck, 2001). In decapod crustaceans, low temperatures in general, but especially in combination with high Mg^{2+} levels in the haemolymph, have been hypothesized to reduce their activity owing to the effect of Mg^{2+} as a relaxant (Frederich, 1999; Frederich et al., 2001). Since Reptantia regulate $[Mg^{2+}]_{HL}$ only slightly below the $[Mg^{2+}]$ of sea water, their scope of activity should be hampered. In contrast, Natantia are known to regulate $[Mg^{2+}]_{HL}$ to very low levels (Tentori and Lockwood, 1990; Frederich et al., 2001). This might explain not only the limits of cold tolerance in decapods, but also their geographic distribution, and might be the reason for the principal absence of the Reptantia from the polar regions (Frederich et al., 2001).

1.4 AIMS OF THIS STUDY

Hypotheses

(i) Physiological constraints limit the distribution of high-latitudinal decapods, e.g. the lack of a sufficient $[Mg^{2+}]_{HL}$ regulation mechanism.

(ii) Some taxa have managed to overcome these physiological constraints using ecological life-history adaptations.

The major aims of this study are

(i) to investigate reproductive traits in Subantarctic caridean decapods and to asses, how ecological adaptations helped to overcome physiological constraints in the cold.

(ii) to study reproductive strategies in Subantarctic lithodid anomurans, and to assess their capability to respond to distribution-limiting physiological constraints by ecological adaptations in early life history.

(iii) to define ecological and phylogenetic limits in life history adaptation to high latitudes, which complement physiological constraints involved into distribution-limiting factors for decapods in Polar areas.

(iv) to work out a perspective for the evolution of the high latitudinal decapod fauna.

2 MATERIALS AND METHODS

2.1 SAMPLING AND STUDY AREAS

2.1.1 Study areas

This work was mainly carried out in the southernmost part of America, the Magellan region, which comprises one of three classical Subantarctic provinces (Fig. 2, for discussion see Hedgpeth, 1971; De Broyer and Jazdzewsky, 1996) and is situated only about 1000 km north of the Antarctic Peninsula. The Antarctic and the Magellan region are separated by the Drake Passage, whose deep-sea trenches reach 5000 m depth. The Antarctic Circumpolar Current (ACC), which is driven by the West Wind Drift, is assumed to be the main oceanographic barrier isolating the Antarctic marine realm from the rest of the marine world. The usually wide ACC is forced through the narrow channel of the Drake Passage. After passing through this channel, the drift again widens greatly and the current splits into two. Its smaller northern branch creates the Cape Horn current and later loops north into the Falkland Current, whereas the larger branch continues eastwards to South Georgia.

The Falkland Current is the reason for the cold-temperate marine realm of the south-western Atlantic Ocean, with its offshore waters extending north to the latitude of Buenos Aires (about 16°S), where it strongly weakens due to the influence of the Brazil Current moving south along the coast. The south-western Atlantic Ocean comprises the second large study area in the present work (Fig. 2). In addition, preliminary studies and observations were carried out along the Subantarctic islands of the Scotia Arc (Fig. 2) including the South Shetland Islands (King George Island), situated at the northernmost tip of the Antarctic Peninsula.

2.1.2 Plankton sampling

Plankton material for the study of meroplankton assemblages as well as larval developments in species of the Campylonotidae and the hippolytid shrimp *Nauticaris magellanica* was obtained from the south-western Atlantic and the Magellan region (Figs. 2, 5) during various cruises. This includes extensive material obtained during the cruise

by the German vessel "Walther Herwig" to the south-western Atlantic Ocean in 1978 (Ciechomski et al., 1979; Cousseau et al., 1979; Publications II, III), as well as the Joint Chilean-German-Italian Magellan "Victor Hensen" Campaign to the channel and fjord system of the cold-temperate subantarctic Magellan region (Figs. 2, 3; Publication VI) in October/November 1994 (see also Arntz and Gorny, 1996).

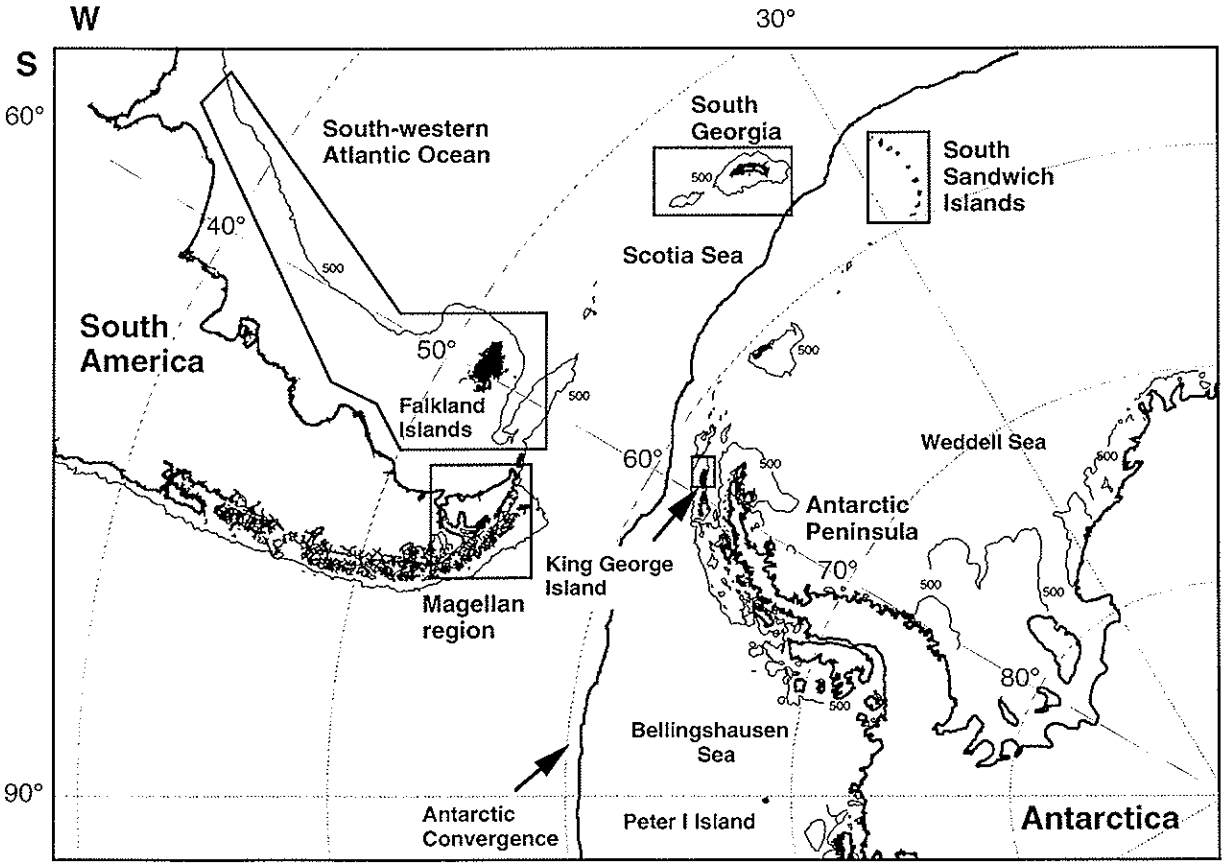


Fig. 2. Study areas (as indicated by boxes) in the Southern Ocean (Antarctica without indication of ice shelves). The 500 m isobath has been marked.

Different pankton nets were used during these cruises (for detailed description of sampling see, Publications II, III, VI). Zooplankton samples were directly preserved in 4 % hexamethylenetetramine-buffered formaldehyde seawater solution. The decapod larvae material for morphological studies obtained during the above mentioned cruises has been compared to the material collected by a plankton net of 200 µm mesh size by monthly sampling from onboard a Zodiac in the Beagle Channel (Tierra del Fuego) from 1987 to 1989 (see Lovrich, 1999).

Sampling of plankton in the Maxwell Bay off King George Island (Fig. 2) was performed by means of a Bongo net of 200 µm mesh size. Sampling was carried out on a weekly basis from January to April 2002 (for details see, Publication IX).

2.1.3 Capture and maintenance of ovigerous females

Ovigerous *Campylonotus vagans* were caught in September 2001 from about 15 to 30 m depth in the Beagle Channel (54°53 S, 68°17 W, Fig. 3) using an inflatable dinghy equipped with an epibenthic trawl (1.7 m mouth width, net with 1 cm mesh size, see Tapella et al., 2002). Additional adults of *C. vagans* for size-fecundity relationships were obtained from various cruises to the Straits of Magellan and the Beagle Channel (see, Publication IV).

Ovigerous lithodid crabs (*Paralomis granulosa*, *Lithodes santolla*) were collected in April/Mai 2000 and 2001 in the Beagle Channel (Tierra del Fuego, southern Argentina) using commercial fishery traps (for details of local crab fisheries, see Lovrich, 1997). Lithodids were maintained at the local institute in Ushuaia (CADIC) and a few weeks after transported with the German research icebreaker "Polarstern" to the marine biological laboratory Helgoland (BAH).

Investigations of the decapod fauna along the Subantarctic islands of the Scotia Arc were performed during the Latinamerican "Polarstern" Study (LAMPOS) on board RV Polarstern in April/Mai 2002. Decapod material was obtained using an Aggasiz trawl at variable depths in waters off the Sandwich Islands (Fig. 2). The shrimp material obtained was sorted and photographed, then fixed in 3-4 % buffered formalin.

Ovigerous females of both lithodids and shrimps were kept in flow-through seawater aquaria (10 to 30 l water content, depending on the species studied) in Argentina (CADIC, Ushuaia) and Germany (BAH, Helgoland) at constant temperatures (for details see, Publiactions III - V, VII + VIII). Lithodids and caridean shrimps were fed twice a week with squid and commercial TETRA AniMin pellets for aquaristics (TetraWerke, Germany), respectively.

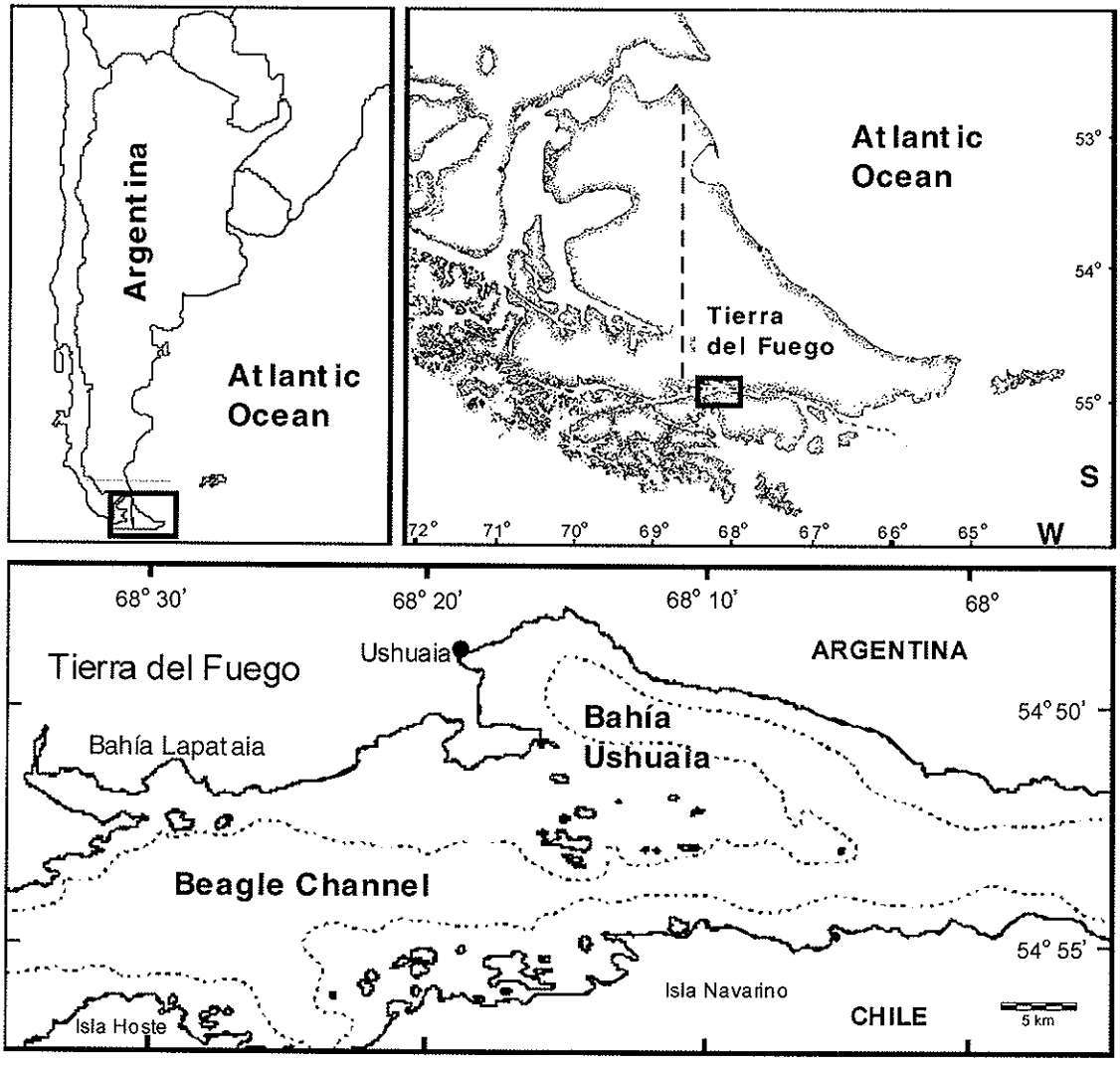


Fig. 3. Main sampling area of ovigerous crabs and shrimps in the Subantarctic Beagle Channel (Magellan region, South America).

2.1.4 Rearing of larvae

Freshly hatched, actively swimming larvae obtained from different females of both lithodids and shrimps, were randomly selected and subsequently reared in individual 100 ml bowls kept under natural conditions of salinity and light (see, Publications III – V, VII + VIII). For the study of temperature tolerance in larval developments in *P. granulosa*, we tested 1, 3, 6, 9, 12, and 15°C. Larvae in each treatment (n = 48 each) usually resulted from the same females. Temperature tolerance in larvae of *L. santolla*

was only tested below 6°C, the average water temperature in the Beagle Channel in spring (Lovrich 1999), i.e. at 1, 3, and 6°C.

Lithodid larvae were reared without addition of food, since previous experiments (McLaughlin et al., 2001, 2003; Calcagno et al., 2004a, b; Kattner et al., 2003) had shown that all larval stages of *L. santolla* and *P. granulosa* are non-feeding. From the day of metamorphosis, juvenile crabs were fed with *Artemia* nauplii. At 9-15°C, the culture water (in juveniles also food) was changed every other day, at lower temperatures every third day. In all treatments, the larvae or juveniles were checked daily for moults or mortality. In the lithodid *P. granulosa*, the rearing experiments with one hatch were continued throughout one year, from August 2001 to August 2002, while all other experiments in lithodids and shrimps were terminated as soon as the crab stage II, or juvenile II, respectively, was reached. Larvae of the caridean *C. vagans* were always maintained in presence of food (*Artemia* sp. nauplii) immediately following hatching, and only in an additional treatment larval resistance of unfed larvae to starvation was tested (Publication IV).

2.2 SAMPLE TREATMENT

2.2.1 Morphological studies

Carapace length (CL) and total length (TL) of caridean larvae and adults were measured from the base of the rostrum between the eyes to the posterior dorsal margin of the carapace, and to the posterior margin of the telson, respectively (Publications I – V, IX). The terminology used for the differentiation of the larval phases, the larval morphology and the characteristics encountered to distinguish between species and larval stages, corresponds to that suggested by Williamson (1960, 1968, 1982).

2.2.2 Total lipid content and fatty acid analyses

Fatty acid composition was determined by gas chromatography (Kattner and Fricke, 1986). In summary, 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 x 0.25 mm i.d. wall-coated open tubular column (film thickness: 0.25 µm; liquid phase: DB-FFAP) using temperature programming. Fatty acids were identified with standard mixtures and quantified by internal standard (Kattner et al., 1998). 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.

2.2.3 Protein analyses

Larvae sampled for protein analyses 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 dry mass (W) was afterwards measured in a Sartoris 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).

2.2.4 Analyses of elemental composition, dry mass (W), carbon (C), hydrogen (H), nitrogen (N)

All larvae sampled for elemental and biochemical analyses throughout larval development in both lithodids and shrimps originated from one single female. Sometimes, parallel rearings from different females are compared. Samples for determinations of W and elemental composition (C, N, H; with n = 5 replicates each; one individual per replicate) were taken immediately after hatching and in variable intervals during later development, depending on the larval developmental pathway in shrimps and lithodid crabs (see, Publications IV, V, VII, VIII). Exuviae were sampled from each larval stage

in order to quantify biomass losses during successive moults. Since a minimum of 0.2 µg dry mass is needed for each elemental analysis, up to 20 exuviae (originating from various females) per replicate sample were pooled.

Weight measurements were carried out to the nearest 0.1 µg with an autobalance (Mettler, UMT 2). Techniques and equipment used for obtaining C, N and H content of larvae and juveniles were the same as described by Anger and Harms (1990).

2.3 DATA ANALYSES

2.3.1 Cluster analyses

We used the software package PRIMER (Plymouth Routines in Multivariate Ecological Research) developed at Plymouth Marine Laboratory, United Kingdom, for station classification of meroplankton data obtained from the Magellan region (Publication VI). The hierarchical agglomerate cluster method (Clarke and Gorley, 2001) was applied on the basis of abundance means per station to differentiate meroplankton communities utilising the Bray-Curtis Similarity Index.

2.3.2 Statistics

The relationship between fecundity and female size (CL) of *C. vagans* was demonstrated with a linear regression analysis (Publication IV; Sokal and Rohlf, 1995) previously log-transforming data to achieve linearity. Significant differences in egg-sizes among the different stages (for classification see, Publication IV) were tested using a one-way ANOVA (Sokal and Rohlf, 1995). Assumptions of homoscedasticity and normality were tested with Bartlett´s and Kolmogorov-Smirnov tests, respectively. For the ANOVA, we pooled the egg-size data of stages I and II because of strong similarity and no variability in stage II.

Differences in larval elemental composition at hatching were compared in different females of both lithodids and shrimps. Statistical differences were tested by means of a one-way ANOVA (Sokal and Rohlf, 1995). Changes in elemental composition (W, C, N, H), protein and total lipid parameters were described and compared with linear regres-

sions in relation to larval age (Sokal and Rohlf, 1995). The elemental and protein data were previously 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 (Publications V, VII, VIII, Sokal and Rohlf, 1995).

3 RESULTS AND DISCUSSION

3.1 PLASTICITY IN CARIDEAN REPRODUCTIVE MODES – A LATITUDINAL VIEW

Many species of caridean shrimps (Natantia) have developed strong life-history adaptations to both latitudinally changing conditions of food and temperature (for review see, Clarke, 1982b, 1987, 1993a). The most conspicuous adaptations include an increasing egg size with increasing latitude and decreasing average water temperature, associated with changes in the biochemical composition of eggs, and often reduced fecundity (Gorny et al., 1992; Wehrtmann and Kattner, 1998; Wehrtmann and Lardies, 1999; Anger et al., 2002; Thatje et al., 2004a). Egg nutrient content has been directly correlated with egg size, assuming that size increase in eggs with latitude should reflect enhanced female energy investment into each embryo (Clarke, 1993a, b; Wehrtmann and Kattner, 1998).

As an additional latitudinal trend, larval size at hatching appears to increase, whereas the number of larval instars and the degree of morphological variability tend to decrease. This is probably best studied in the hippolytid shrimp *Nauticaris magellanica* (cf. Wehrtmann and Albornoz, 1998; Thatje and Bacardit, 2000c), which shows a distribution along approximately 35° of latitude, from central Chile south to the Magellan region (Spivak, 1997). Differences in developmental pathways of larvae of this species reared in the laboratory compared to material from the plankton suggest variability in larval development to be a direct response to stress (Wehrtmann and Albornoz, 2003; Thatje and Bacardit, 2000c). This might be referred to variable natural conditions, since it has been frequently shown that caridean morphogenesis is affected by distinctive biotic and abiotic factors in the field, such as temperature, salinity, and food availability (Christiansen and Anger, 1990; Thatje and Bacardit, 2000c; Anger, 2003).

Low temperatures at high latitudes have been observed to retard not only larval development time, but also larval growth and to reduce mortality as compared with boreal species (Clarke and Lakhani, 1979; Gorny et al., 1993). The requirements for exogenous energy from food allowing for developmental flexibility and extended modes of

larval development in the cold should therefore be high, as metabolic costs for additional moults as well as energy losses with cast exuviae imply a high degree of dependence on plankton productivity (Anger, 2001; Wehrtmann, 1991). Nevertheless, the flexibility in larval developmental pathways also allowed carideans to evolve energy saving strategies when low temperatures and limited food availability selected for abbreviated and partially endotrophic modes of larval development (Thatje et al., 2001). The need for energy saving strategies at conditions of low temperatures and a seasonally limited primary production in high latitudes has suppressed the extent and flexibility of developmental pathways in caridean larvae. For instance, strongly abbreviated larval developments passing invariably through only 2 or 4 larval instars, respectively, in the sub- and high Antarctic genera *Campylonotus* and *Chorismus* (Table 2; Bruns, 1992; Thatje et al., 2001; Thatje and Lovrich, 2003; Thatje et al., 2004a), combined with high larval resistance to starvation, especially in the zoea I instar (Thatje et al., 2004a, b), allow for an enhanced synchronisation with short and pulsed periods of primary production, and reduce at the same time the degree of larval dependence on planktonic food sources (Clarke, 1988; Anger et al., 2003). Further energy saving strategies are low metabolic and elemental losses (C, H, N) during few moults and by very thin exuviae (Thatje et al., 2004b).

Conclusions

- Plasticity in caridean larval developments allows for energy saving traits through abbreviated larval developments in high latitudes.
- This enhances the possibility of synchronizing larval development with short periods of primary production.

Similar early life history adaptations are known also from the Antarctic crangonid *Notocrangon antarcticus* (Bruns, 1992). In the high Antarctic Weddell Sea, carideans spawn only every second year (Arntz et al., 1992; Gorny et al., 1992; Gorny and George, 1997), suggesting insufficient energy supply to female reproduction due to short periods of primary production during summer, whose length may not be sufficient for the level of somatic growth allowing for an annual reproductive cycle (Clarke, 1982a). In polar environments, the mismatch between energy availability and high costs for female energy investment into large embryos may thus have selected against

complete lecithotrophy in caridean larval development (Thatje et al., 2003a). On the other hand, complete endotrophic larval developments of pelagic larvae are rare in marine caridean shrimps anyway, which may indicate a phylogenetic constraint for the evolution of lecithotrophic developments in the sea. One exception are the Palaemonidae from freshwater habitats, which have endotrophic larval developments (cf. Magalhães 1988; Odinetz Collart and Magalhães, 1994). However, this family is predominantly distributed from tropical to temperate regions (Hunte, 1978; Delgado et al., 1997) indicating temperature as an additional phylogenetic constraint for lecithotrophic larval developments. One known exception, which should be mentioned here, is the subarctic *Sclerocrangon boreas*, which has a direct and abbreviated (lecithotrophic) development of benthic larvae, including a high degree of parental care (Makarov, 1968; Miglavs, 1992).

The hypothesis, presented here is supported by some biochemical observations on lipid and fatty acids in polar shrimps. Clarke (1977a, b) stated that despite some increase in muscle phospholipid content *Chorismus antarcticus* did not show a considerably different lipid content and fatty acid composition as compared to crustaceans from lower latitudes. Consequently, he suggested that the Antarctic marine environment has little effect on the biochemical composition of adult shrimps (Clarke, 1977b, c). The lack of wax esters in *C. antarcticus* as well as in *Campylonotus vagans* from the Subantartic Magellan region (Thatje et al., 2004b) may also suggest that this pattern coincides with an inability of further energetic adaptation to low temperatures.
Recently, Graeve and Wehrtmann (2003) found that the fatty acid and lipid contents of polar shrimp eggs do not differ significantly from those of tropical species. This was surprising, because previous studies suggested that high latitudinal crustacean eggs, which are generally larger, have a higher nutrient content per embryo (Clarke, 1993b), as the adult Antarctic shrimps appear to accumulate large amounts of lipids (Clarke, 1983, 1987). Due to lack of data and the low number of caridean species living in the Southern Ocean, a general conclusion is still difficult. Inter- and intraspecific nutrient contents in eggs are highly variable, and should directly reflect feeding conditions (Herring, 1974; Hopkins et al., 1993; Anger et al., 2002). Estimates and comparisons of lipid contents from eggs, in particular, are problematic, since they do not always consider the developmental stage of embryo development (variable degree of lipid depletion).

Large eggs rich of lipids, therefore, do not necessarily imply a higher degree in endotrophy of the larvae, but without doubt should indicate large and advanced larvae at hatching (Wehrtmann and Kattner, 1998; Thatje and Bacardit, 2000c; Thatje et al., 2001; Thatje et al., 2004a). In addition, it should be considered that energy contents of eggs are also dependent on nutrient density, which is somehow independent of egg size (Anger et al., 2002).

Conclusions

- The lack of lecithotrophic larval developments in marine Caridea is suggested to be a phylogenetic constraint.

3.2 REPTANT DECAPODS IN THE SOUTHERN OCEAN

3.2.1 Antarctic reptant decapods: only a myth?

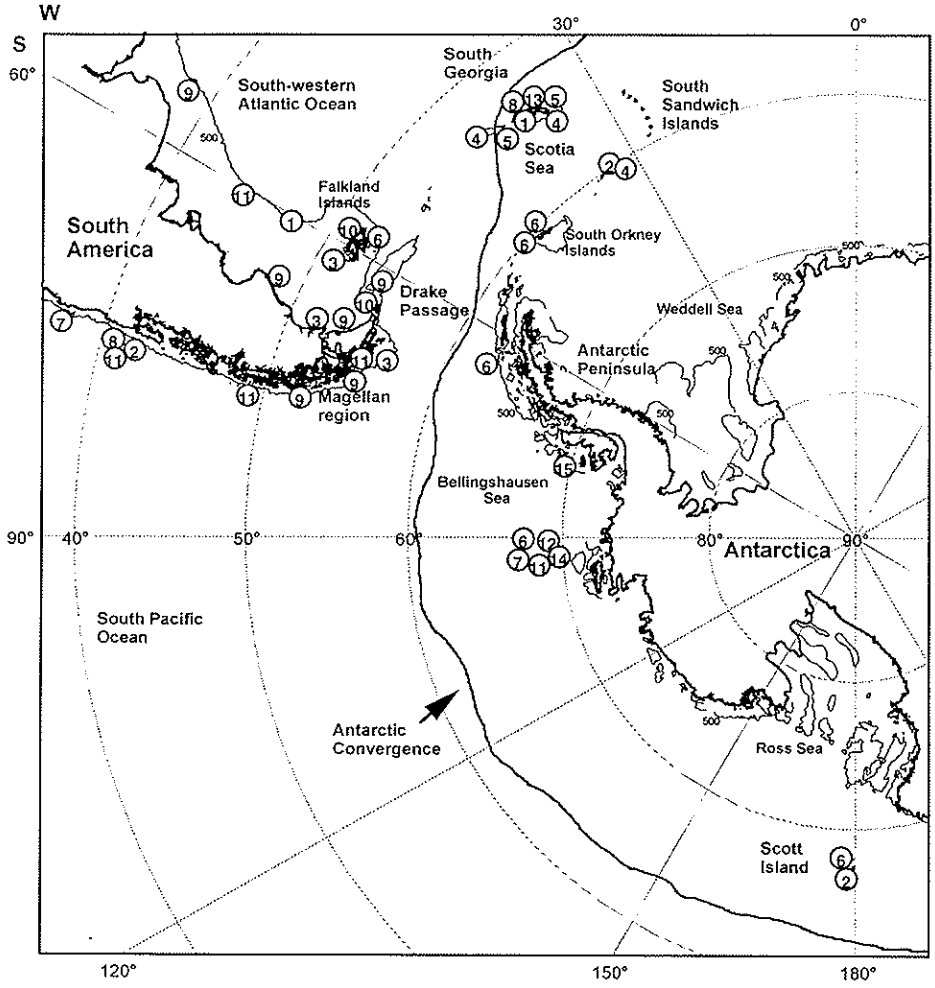
THE EVIDENCE

"Everybody who has worked in Antarctic waters has been struck by the peculiar absence of crabs, lobsters, shrimps ..... in shallow waters"

H. Broch, 1961

The impoverished Antarctic decapod fauna, compared with the high diversity of decapod crustaceans recorded in the Subantarctic (Gorny 1999), still comprises one of the most enigmatic phenomena in marine biodiversity research. Although Broch (1961) described the decapod diversity pattern in the Southern Ocean at the very beginning of modern Antarctic research, his statement was not strictly correct, since the first Antarctic Natantia (*Chorismus antarcticus*, *Notocrangon antarcticus*) were already discovered by the Expedition of the German Polar Commission to South Georgia in 1882-83 (Pfeffer, 1887). However, South Georgia is a rather Subantarctic environment. Since then, a couple of new species and records were reported from the Southern Ocean (e.g. Yaldwyn, 1965; Kirkwood, 1984; Tiefenbacher, 1990; Thatje, 2003), but Antarctic

decapod diversity, apparently, remained poor, represented by about a dozen natant (caridean shrimp) species only, some of which are actually known to occur in high abundances and large collections on the high Antarctic Weddell Sea shelf (Arntz and Gorny, 1991; Arntz et al., 1992; Gorny, 1999).



Paralomis anamerae	①	*Lithodes confundens*	⑨
P. spectabilis	②	*L. santolla*	⑩
P. granulosa	③	*L. murrayi*	⑪
P. formosa	④	*L. turkayi*	⑫
P. spinosissima	⑤	*L.* sp. undet. 1	⑬
P. birsteini	⑥	*L.* sp. undet. 2	⑭
P. tuberipes	⑦	*P. sp.* undet. 1	⑮
Neolithodes diomedeae	⑧		

Fig. 4. Lithodid records in the Southern Ocean (Antarctic without indication of ice shelves; 500 m isobath has been marked). Informations obtained from the literature: Takeda and Hatanaka, 1984; Báez et al., 1986; Boschi et al., 1992; Retamal, 1981, 1992; Klages et al., 1995; Arana and Retamal, 1999; Gorny, 1999; Collins et al., 2002; Zaklan, 2002; Thatje and Arntz, 2004, and references therein).

The controversial discussion of whether reptants, especially brachyuran and anomuran crabs, are present at least with some members in the Antarctic (Yaldwyn, 1965; Dell, 1972; Gorny, 1999; Frederich et al., 2001, and references therein), resulted from Stebbing´s record of the brachyuran crab *Halicarcinus planatus* (Stebbing, 1914) from Macdougal Bay, South Orkney Islands (Fig. 4). This material was probably collected during the Scottish National Antarctic Expedition in 1903, and Stebbing´s record was based on museum material only. Yaldwyn (1965) was the first to doubt that the occurrence of *H. planatus* at the South Orkney Islands is possible. Although this species living mostly in the intertidal to shallow subtidal is a very common representative in the Magellan region, including the Falkland Islands, and representatives of the genus are distributed circum-Subantarctically (Gorny, 1999), it has never been found at South Georgia, which is situated much north of the South Orkney Islands and north of the ACC (Fig. 6). Frederich (1999) supposed *H. planatus* to be a potential invader of the Antarctic, due to low Mg^{2+} contents in its haemolymph, which is untypical of crabs (Frederich et al., 2001); the extended larval development through completely planktotrophic larvae, however, should select against this species in the Antarctic environment (Boschi et al., 1969; Thatje et al., 2003a). This could already have impeded the occurrence of *H. planatus* at South Georgia, although a colonisation through larvae by means of currents should be, theoretically, possible. My own investigations at three locations along the north-eastern coast of South Georgia in summer 2001 did not reveal any intertidal brachyuran crab. On the basis of our recent knowledge, we should seriously doubt the record of *H. planatus* from the South Orkney Islands by Stebbing (1914), which was presumably due to mislabelled museum material (see also, Yaldwyn, 1965).

Larvae of benthic reptants were first reported by Tiefenbacher (1994), who found five mesopelagic larvae of the palinurid *Stereomastis suhmi* between 400 to 800 m sampling depth. Tiefenbacher supposed the occurrence of palinurid larvae to be reason of adult populations in the deep waters of the sampling area (Drake Passage, 57°08,5S; 55°0,60´W), which remains uncertain. However, larvae and adults of *S. suhmi* have been reported from the Magellan region (Arntz et al., 1999; Thatje et al., 2003a) and at about 2100 m depth on the continental slope south of the Beagle Channel (Arntz et al., 1999). These records suggest that the occurrence of adult *S. suhmi* in the deep of the Drake Passage might be possible.

Recently, reptant larvae of the genus *Pinnotheres* (Brachyura) and the mole crab *Emerita* sp. (Anomura) have been recorded in Maxwell Bay (King George Island, 62°14´33S; 58°43´81W) at the Antarctic Peninsula (Thatje and Fuentes, 2003), to be considered as the first records of reptant larvae south of the Polar Front. This record was discussed to be due to the intrusion of Subantarctic water masses into the Antarctic regime, as evidenced by the accompanying Subantarctic copepods (genus *Acartia*), and not due to established adult populations in the Antarctic.

The first certain record of an adult reptant from the high Antarctic marine realm, a lithodid anomuran from the South Pacific side of the Antarctic, was published by Birstein and Vinogradov (1967). This first find of *Paralomis spectabilis* off Scott Island (67°23´S; 179°53´E), was realized during the Russian expedition on board the oceanographic vessel "Ob" to the Southern Ocean in summer 1957-58. However, it should be considered that Hale (1941) had already found *Lithodes murrayi* off Maquarie Island some years in advance of the Russian colleagues, but at lower latitude (58°28´S; 158°53´E). Later, an additional record of three lithodid anomurans from the Southern Pacific (about 67°29´S; 179°55´W), at about 1080 m water depth, was described as *Paralomis birsteini* by Macpherson (1988a).

The various records of lithodid crabs from the Southern Ocean raised fishery expectations (although ecologists always considered these single finds as exceptions!), since these crabs were known as a fishery resource around the Subantarctic island of South Georgia, where at least five lithodid species are known to occur (Otto and Macintosh, 1996; Collins et al., 2002, and references therein; Fig. 4). The catch of 88 specimens of *Paralomis birsteini* along the Antarctic Peninsula, from the South Orkney Island southward to Peter I Island in the high Antarctic Bellingshausen Sea using commercial "centolla" baited traps (Fig. 4; Arana and Retamal, 1999), as well as the records of *Lithodes murrayi* off Peter I Island (180-260 m water depth, Klages et al., 1995), clearly demonstrated the existence of lithodid anomuran populations in the Antarctic (Thatje and Arntz, 2004). The potential value as a fishery resource must be considered low due to delayed first maturity and slow growth, as that of shrimp populations in the Antarctic (Arntz et al., 1994). It should be commented here, that the taxonomic status of *P. birsteini* in the work by Arana and Retamal (1999) remains uncertain, since both authors confounded this species with *P. anamerae* in their Table 1 (Arana and

Retamal, 1999). It should be stressed that the lithodid record by Klages et al. (1995) suggested their occurrence to be related with temperatures above 0°C at the seafloor (+1.8°C in their study), and this might explain the absence of records of lithodid anomurans from the colder Weddell and Lazarev Sea shelves (always below 0°C, see, Seabrooke et al,. 1971; Arntz et al. 1992).

Conclusions

- Lithodid anomurans comprise the only reptant group apparent with adult populations in the Antarctic except the high Antarctic continental shelf, where temperatures drop permanently below critical temperatures for lithodids.

3.2.2 Reproductive modes in Southern Ocean lithodid anomurans

Embryonic development, larval release, and parental care. Larval release in decapods is known to occur frequently in response to abiotic environmental conditions such as lunar or tidal cycles, leading to synchronised hatching which usually does not exceed a period of a few hours to days (DeCoursey, 1983; DeVries et al., 1983; Saigusa and Kawagoye, 1997; Zeng and Naylor, 1997). Although aquatic invertebrate embryos are usually tolerant of low oxygen concentrations, egg-masses are size-limited due to internal oxygen gradients (Strathmann and Strathmann, 1995). Decapods, which produce compact egg-masses of up to several centimetres in diameter, compensate oxygen deficiency in the centre of their egg-masses mainly by abdominal flapping. This maternal care behaviour tends to increase during late embryonic development when the oxygen demand of the embryos increases (Nakanishi, 1985; Naylor et al., 1999; Fernández et al., 2000; Baeza and Fernández, 2002). The energetic cost of brooding depends mainly on the size of the egg-mass and on oxygen partial pressure. Since the oxygen partial pressure in seawater is temperature-dependent, these costs should be higher in temperate and warm shallow subtidal zones than in the deep sea and at high latitudes.

In cold environments such as the Antarctic and adjacent Subantarctic regions, the hatching mode of decapods is little known. The two most common lithodid representatives from the Subantarctic Beagle Channel off Tierra del Fuego, *P. granulosa* and *L. santolla*, are known to carry up to 10,000 and 32,000 eggs per clutch, respectively (Lovrich, 1997). Embryonic development in these species is known to last between about one to almost two years (*L. santolla*: 9-10 months, Vinuesa, 1984; *P. granulosa*: 18-22 months, Lovrich and Vinuesa, 1993). Hatching of larvae in low daily numbers results in extended hatching periods, which can last at least up to 2 months in duration (Thatje et al., 2003). Freshly hatched larvae of *P. granulosa* showed low oxygen consumption rates at low temperatures (Thatje et al., 2003). The rate, however, strongly increased with temperature, and a similar pattern was already reported in other lithodid species (Nakanishi, 1985; Anger, 1996). Low larval oxygen consumption may be a consequence of low temperature regimes and restricted maternal aid in oxygen supply due to the physiological constraints at low temperatures. Namely, reptant crabs may suffer from narcotising effects induced by low temperatures in combination with high Mg^{2+} levels in the haemolymph (Frederich et al., 2001). As a consequence, brooding activities such as abdominal flapping, which is needed for active and controlled larval release, should be dramatically reduced. Low daily hatching rates are therefore suggested as an ecological response to the physiological constraints (the lack of strong abdominal flapping, Baeza and Fernández, 2002) and consequently low energetic costs for the female.

If we assume that embryonic development duration in decapods is not strictly genetically determined, but also dependent on temperature and oxygen level (oxygen availability), oxygen gradients in egg-masses of reptant decapods could be responsible for the delay of hatching of larvae from the innermost layers of the egg-mass (Chaffle and Strathmann, 1984), thus explaining the occurrence of extended hatching periods.

Conclusions

- In Subantarctic lithodids, long-lasting embryonic development, and larval hatching in low daily numbers over an extended period of up to several weeks depending on hatch size, are discussed as life history adaptations to, and/or physiological constraints by, the environmental conditions of high latitudes.

Larval development. The southern stone crab, *P. granulosa*, shows complete lecithotrophy and a strongly abbreviated larval development with two zoeal stages and a megalopa (Calcagno et al., 2003, 2004). These reproductive patterns are strikingly similar to those observed in another lithodid crab from the Subantarctic Beagle Channel, the southern king crab, *L. santolla* (Molina), which has three zoeal stages and a megalopa (McLaughlin et al., 2001; Lovrich et al., 2003). Both species occur in the Magellan region, where strong seasonality in the light conditions and low average temperatures are typical, allowing for only a short period of primary production. In both species, hatching of larvae occurs in winter (July-September, Lovrich and Vinuesa, 1999; Thatje et al., 2003). According to larval development duration at about 5-6 °C, which is the average water temperature in the Beagle Channel in late winter (Lovrich, 1999), metamorphosis and first food uptake of the actively feeding benthic juvenile should occur in spring (September-November), when primary production increases (Anger et al., 2003).

The patterns of larval and early juvenile development as well as changes in biomass and chemical composition observed in *L. santolla* can be compared with those previously described for a congener from the North Atlantic, *L. maja* (Anger, 1996). Both closely related but geographically separated Subpolar species show a number of striking similarities not only in their adult ecology and climatic distribution but also in early development. Both pass through three zoeal stages and a megalopa, and comparison of development duration, larval survival, and changes in biomass and chemical composition of fed and unfed larvae shows that both species have endotrophic larval developments (Lovrich et al., 2003). Total duration of larval development at 6°C in *L. santolla* was about 10 weeks, whereas *L. maja* required about 7 weeks at a rearing temperature of 9°C. This suggests similarity also in the temperature dependence of development duration (Anger et al., 2003).

The most striking similarity between *L. santolla* and *L. maja* is in the complete lecithotrophy from hatching through all four larval stages to metamorphosis, which is interpreted as adaptation to Subpolar environments. The mismatch of short planktonic food availability and long pelagic development in cold waters should have selected for a food-independent mode of larval development, which is principally based on an enhanced energy allocation to female reproduction (for recent discussion, Anger, 2001).

Lecithotrophy has recently been observed also in a congener from the North Pacific and the Bering Sea, the golden king crab, *L. aequispinus* (Shirley and Zhou, 1997), which suggests that this may be a wide-spread developmental pattern in *Lithodes* species living at high latitudes.

An extremely high C:N ratio in both *P. granulosa* and *L. santolla* at hatching (the same as in *L. maja*, Anger, 1996) indicates that large lipid reserves persist in both species from the egg yolk (Lovrich et al., 2003; Kattner et al., 2003; Calcagno et al., 2004), serving the larvae as an energy-rich fuel for endotrophic development under conditions of strongly limited food availability. In both species, the C:N ratio decreased significantly during larval development, which indicates a preferential degradation of lipid reserves, especially during the zoeal (i.e. more active) phase of development, coinciding with a weaker decrease in the protein pool (cf. Anger, 1996). As another similarity between these species, the first juvenile crab stage showed immediately after metamorphosis food uptake and rapid growth. A particularly steep increase in the C:N ratio during the postmoult and early intermoult periods suggests a rapid replenishment of lost lipids. In addition, however, cuticular mineralization with inorganic carbonates may contribute to this increase in the C:N index. Decreasing values thereafter indicate in both species a proportionally stronger increase in the protein fraction, reflecting epidermal reconstruction and growth of muscular and nervous tissues during the premoult period. All these patterns are typical of planktotrophic larval and juvenile crab stages (for recent review, see Anger, 2001).

However, the degree in adaptation to lecithotrophic larval developments differs between *L. santolla* and *P. granulosa.* Larvae of *L. santolla* contain higher amounts of fatty acids and protein than *P. granulosa.* In addition, in *L. santolla* these energy sources in form of lipids (mainly triacylglycerol) are less utilised until metamorphosis, whereas *P. granulosa* almost exhausts all lipidic energy pools (Kattner et al., 2003). Monounsaturated fatty acids are dominating in *L. santolla* in contrast to *P. granulosa*, and are preferably utilised as compared to polyunsaturates (Kattner et al., 2003).

Besides principal similarities in the patterns of larval development and in associated chemical changes within biomass of *P. granulosa* and *L. santolla*, there are similarities in larval behaviour of these species. In both, the zoeal stages are slow but active

swimmers, showing a tendency to stay near the bottom as demersal larvae (Thatje et al., 2003). The same applies to the megalopa during the first 2-3 days after moulting. Subsequently, however, the megalopa becomes fully benthic and increasingly sluggish. Generally low locomotory activity of the larvae may be an energy saving mechanism during non-feeding development, representing another adaptation to food-limited environments.

As an additional tentatively adaptive trait, the larval stages of both species show very low exuvial energy losses as compared with planktotrophic decapod larvae, which is the same as in *L. maja* (for recent discussion of the literature, Anger, 1996, 2001). Production of unusually thin exuviae was observed also in a terrestrial brachyuran crab species with non-feeding larvae (Anger and Schuh, 1992), suggesting that similar energy-saving traits may occur in various decapod crustacean taxa with a lecithotrophic mode of development.

It is suggested that food-independent larval development may be an important life-history adaptation to limited primary production in Subantarctic marine environments. This trait may partially explain the wide range of bathymetric distribution of some Subantarctic lithodid species from the shallow sublittoral to the deep sea (Báez et al., 1986; Lovrich and Vinuesa, 1993), where scarce planktonic food availability presumably selects against an extended planktotrophic larval development. Similar patterns may thus be expected to occur also in other lithodids from high latitudes, for instance in *L. aequispinus.*

Conclusions

- *Lithodes santolla* and *Paralomis granulosa* are able to complete their larval development without external food supply, i.e. the larval development is completely endotrophic.
- Physiologically, *L. santolla* shows a better adaptation to the lecithotrophic larval development as compared to *P. granulosa*.
- Complete lecithotrophy in larval developments is an adaptation to scarcity in food availability due to short periods of primary production prevailing in Subantarctic environments.

Temperature tolerance in larvae and early juveniles. Most striking is the wide range of temperatures tolerated by larval and early juveniles of *P. granulosa* (Anger et al., 2003; Publication VIII). At a temperature as low as 1°C, about one half of the larvae developed successfully to the megalopa stage, and metamorphosis to the first juvenile crab stage was reached within a tolerance window ranging from 3-15°C. This suggests that complete mortality before metamorphosis observed in a previous study (Vinuesa et al., 1989) was caused due to either weakness of the larval material or poor rearing conditions (Calcagno et al., 2004). Tolerance of low temperatures was also observed in *L. santolla* (Fig. 5). At 1°C, the moult to the zoea III succeeded, but without reaching the metamorphosis, which could also have been hampered by the low number of replicates used (n = 48).

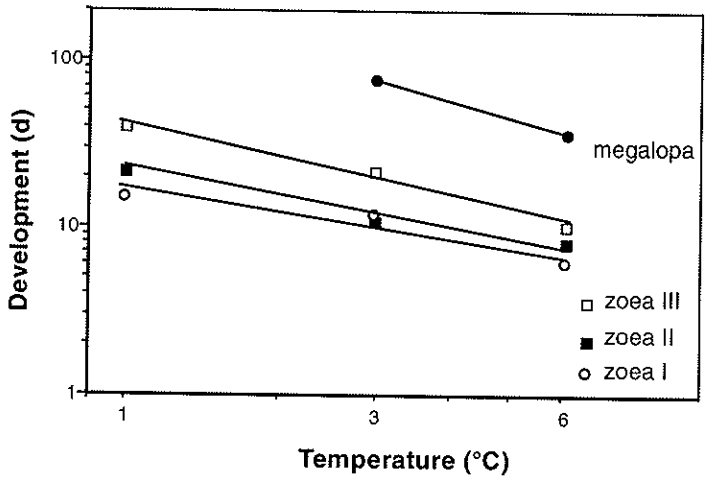


Fig. 5. *Lithodes santolla*. Duration of larval development in relation to low temperature (zoea I - zoea III and megalopa).

Since experimental data suggest an optimum of about 6-9°C for larval developments in both species, the larvae and juveniles appear to be optimally adapted to the temperature conditions at hatching in late winter (Lovrich, 1999). In the natural environment of the Beagle Channel, larvae should become megalopae 2-3 weeks after hatching (late July-August), and metamorphosis to the first juvenile crab should be expected to occur throughout spring/early summer (September-November). One year after hatching from the egg, the juveniles of *P. granulosa* should reach approximately crab instars VI-VII (Anger et al., 2003; Publication VIII).

The tolerated range for larval development in *P. granulosa* is much wider than would be required within the Beagle Channel (summer average 9.8°C, Lovrich, 1999). This tolerance of relatively warm conditions (up to at least 15°C) indicates that *P. granulosa* is not really a typical "cold-adapted", i.e. cold-stenothermal, but actually a cold-eurythermal species (cf. Pörtner et al., 2000; Pörtner, 2002). This is consistent with its broad geographic distribution in the Subantarctic region and along both sides of southern South America, ranging in the Atlantic north to Santa Catarina, Brazil (Boschi et al., 1992), and in the Pacific to the Island of Chiloé, Chile (Retamal, 1981). Likewise, this response pattern is congruent with the observation that *P. granulosa* is the only species of its genus that inhabits also shallow coastal waters where temperatures may be quite variable (Macpherson, 1988b).

The thermal response pattern of the early life-history stages of *Paralomis granulosa* may be typical of the Lithodidae (or at least *Paralomis* and *Lithodes* spp.) living at high latitudes, commonly with wide ranges of geographic and bathymetric distribution (for references see, Paul et al., 2002); true deep-sea species living in a more stable environment, in contrast, should be cold-stenothermal. Since larvae and juveniles of *P. granulosa* are cold-eurythermal, they should be an interesting subject for testing the physiological hypotheses of thermal tolerance recently proposed by Pörtner (2001, 2002). These would suggest that this species, including its early life-history stages, should be capable of regulating mitochondrial densities and/or capacities to produce energy, adjusting to seasonally, bathymetrically, or regionally changing temperature conditions, or after differential acclimatization in the laboratory.

Also extremely long periods of larval development at low temperatures (<6°C), passed without any uptake of food, but based on a degradation of internal energy reserves alone (Calcagno et al., 2003; Kattner et al., 2003). Although an extended lecithotrophic period under conditions of cold indicates also low rates of metabolic energy consumption, successful non-feeding development through a period of up to four months remains highly remarkable (Anger et al., 2003).

Similar patterns are known in *L. maja* from the North Atlantic (Anger, 1996), as well as in a Pacific congener, *L. aequispinus* (Shirley and Zhou, 1997). In the latter species, the maximum period of non-feeding larval development (148 days at 3°C; Paul and Paul, 1999) exceeds even by one month the maximum time that we observed in *P.*

granulosa. Successful larval development at 9°C as well as a wide geographic distribution range (from Japan to the Bering Sea, Canada and Alaska, Zaklan, 2002) suggest that *L. aequispinus* is, like *P. granulosa*, an eurythermal rather than a cold-stenothermal species. The occurrence of ovigerous females of *L. maja* in coastal waters of Greenland, where water temperatures between –1°C and 5°C were recorded (Woll and Burmeister, 2002) suggests a similar cold resistance in its early life-history stages as in *P. granulosa* and, probably, in *L. aequispinus*. Although no temperature tolerance data of larvae are available from this species, the early life-history stages should be eurythermal, as suggested by the wide geographic distribution from the southern North Sea to Spitzbergen, Iceland, and Greenland (Zaklan, 2002). In contrast to endotrophic larval developments, zoeae of the commercially most important lithodid from high latitudes, *Paralithodes camtschatica* (Stevens, 2002; Sundet and Hjelset, 2002), are known to require planktonic food (e.g. Kurata, 1960; Paul and Paul, 1980), although larvae tolerate a wide range from low to moderate temperatures (0-15°C; Shirley and Shirley, 1989).

Although intraspecific variability in cold tolerance may be high in lithodids, similarities among various species suggest that a combination of larval eurythermality and lecithotrophy may be a wide-spread trait in lithodids. Phylogenetic constraints not generally allowing for an evolution of such special adaptations in other reptant Decapoda (for discussion see Thatje et al., 2003a) may have contributed to both gradients of decreasing species richness and the tendency towards a reduction of the larval phase with increasing latitude, which is known as "Thorson´s rule" (Mileikovsky, 1971, based on Thorson, 1936, 1950).

Conclusions

- Both *L. santolla* and *P. granulosa* are well adapted to thrive under conditions of food limitation and cold occurring in high-latitude marine ecosystems. On the other hand, both species are equally well adapted to cool temperate regions, where a relatively elevated temperature level excludes truly cold-adapted stenothermal species. Thus, a remarkable extent of larval eurythermality, together with an unusually high endotrophic potential, allow in these species for extended periods of completely food-independent development from hatching through metamorphosis.

3.2.3 Challenging the cold: the return of crabs to the Antarctic?

The origin of benthic marine invertebrates from both Antarctic and Subantarctic waters can be traced back as far as the Early Cretaceous, about 130 Ma ago (Crame, 1999). At the Late Cretaceous-Early Cenozoic boundary, the austral Province showed temperate aspects in its marine invertebrate fauna, as evidenced by the fossil decapod record (Feldmann et al., 1997; Crame, 1999). At present, the decapod crustaceans are one of those invertebrate groups which display a remarkable reduction in diversity towards high southern latitudes, with about 120 benthic shrimp and crab species in the Subantarctic, compared with only about 5 shrimp representatives remaining on the Continental Shelf of the high Antarctic Weddell Sea (Gorny, 1999; Arntz, 1999). Faunal impoverishment and particularly the final extinction of crabs until about 20 Ma ago (Forster et al., 1987; Clarke and Crame, 1989; Feldmann et al., 1997) is discussed as a result of various processes involved. Antarctic cooling started as late as 35 to 23 Ma years ago as a result of continental drift (Barker et al., 1991). The opening of the Drake Passage created the ACC, which acts as an oceanographic barrier (Crame, 1999). These geological processes affected in particular decapod diversity. Decapod crabs are especially sensitive to cold temperatures. Cold tolerance requires, in the first place, an adjustment of the functional capacity of oxygen supply mechanisms like ventilation and circulation (Pörtner, 2002). In brachyuran crabs this process is hampered by their special sensitivity to Mg^{2+}, combined with their poor ability to reduce Mg^{2+} levels in the haemolymph below those in the water. In consequence, their scope for aerobic activity is minimized and they are narcotised by a combination of temperatures much below 0°C and by high Mg^{2+} levels in the haemolymph (Frederich et al., 2001). Such physiological constraints affect all processes demanding aerobic energy, including brooding in crab species (Fernández et al., 2000), and make them less competitive with those crustaceans, which show the ability to regulate Mg^{2+} at low levels, such as shrimps, isopods and amphipods (Frederich et al., 2000; Tentori and Lockwood, 1990). Furthermore, glaciation events of the Antarctic continental shelf may have affected especially most brachyuran crab species with a limited bathymetric distribution range (Gorny, 1999). Eurybathic species with a refuge in deeper waters, such as most carid-

ean shrimps of the Southern Ocean, were able to re-colonise the shelf (Gorny, 1999). This may explain why Antarctic invertebrates, in general, show a wider bathymetric distribution than species in other regions (Brey et al., 1996).

Recently, king crabs (Lithodidae), which were recorded for the first time only between 13 to 25 million years ago (Cunningham et al., 1992), were discovered in the deeper waters off the continental shelf in the high Antarctic Bellingshausen Sea (Klages, et al., 1995; Arana and Retamal, 2000; Thatje and Arntz, 2004) and in the South Pacific off the Ross Sea (Mcapherson, 1988, cf. chapter 3.2.1.), re-opening the debate about the return of this group to Antarctic waters after glacial retreats (Anger et al., 2003). Our evidence suggests that lithodid crabs are adapted in their life history to physiological constraints in the cold (cf. chapter 3.2.2.). Extended, food-independent larval development periods at low temperatures should be typical of the Antarctic regime, providing independence from scarce and strongly seasonal food availability due to highly seasonal plankton production (Clarke, 1983; Kattner et al., 2003). At the same time, metabolism is minimised during a slow and long-lasting larval development of at least 4 months (cf. chapter 3.2.2., Publication VIII).

This evolutionary young taxon of anomuran crabs, which is represented by several species in high latitudes of both hemispheres and also appears to be a common deep-sea representative (Báez et al., 1986; Macpherson, 1988a, b; Lovrich et al., 2002; Anger et al. 2003, and references therein), is obviously about to liberate itself from the apparent phylogenetic constraints of their ancestor reptants, the limited potential for abbreviated larval developments (cf. chapter 3.2.1., Publication VII), to conquer the polar marine realm as a life habitat. Under present climate conditions, I hypothesise a colonisation pattern of the Antarctic by lithodid crabs via the deep sea, which should have been facilitated by similar ecological conditions found in both cold regions and deep-sea environments (for discussion see, Thiel et al., 1996).

The recent find of Subantarctic reptant decapod larvae at the Antarctic Peninsula off King George Island (cf. chapter 3.2.1.) suggests that crossing the ACC by means of water masses is a possible transport mechanism for meroplanktonic larvae. Although at present low temperatures in the Antarctic should select against insufficiently adapted

larvae, in the case of climate change the re-colonisation of the Antarctic environment by reptants, in particular brachyurans, might be possible, and could be much faster than previously expected (Arntz, 1999; Crame, 1996, 1997).

Conclusions

- The fossil record evidences the extinction of reptants from the Antarctic during Antarctic cooling.
- Comparability of life history adaptations needed for deep-sea and polar environments suggest lithodids to have invaded the Antarctic marine realm via the deep sea.

3.3 FUTURE PERSPECTIVES

There is still a substantial lack in knowledge of reproductive strategies of marine invertebrates in general, which holds especially true for the Southern Ocean. Since the first comprehensive attempt of developing an ecological concept of latitudinal patterns in invertebrate reproduction (Thorson, 1936, 1950; Mileikovsky, 1971), and despite many attempts to dismiss Thorson´s concept (for discussion see Arntz and Gili, 2001), our knowledge of invertebrate reproductive strategies from the Polar regions is improving only slowly. It may take some more time until we can offer comprehensive evolutionary concepts for the origin of the Antarctic fauna and sound ecological reasons for the (non-) existence of taxa in (sub) polar waters. In the following, I would like to outline some future research necessities:

(i) The lack of information on invertebrate reproduction from both the high and Subantartic environments requires a significant increase in autecological studies of invertebrate reproductive traits from all taxa. This should, among other improvements, allow for a better future identification of meroplanktonic larvae in the field, which is urgently required for ecological work.

(ii) Physiological response in early life history of invertebrates to Polar conditions remains almost unstudied. Physiological concepts of cold adaptation are mostly based on adult physiology (Peck, 2001), despite the fact that environmental

conditions, in a first stage, should predominantly select against the more sensitive larvae (Hoegh-Guldberg and Pearse, 1995; Anger, 2001).

(iii) For further elucidation of evolutionary pathways and the origin of the Antarctic fauna, for example the decapod fauna, we have to strengthen circum-Antarctic comparisons and the use of the molecular tool. For instance, it is still uncertain whether decapods have predominantly invaded the Antarctic via the deep sea (as herein suggested for the lithodid fauna) or used the Subantarctic islands as biogeographic step-stones (e.g. the islands of the Scotia Arc). Genetics should help to elucidate evolutionary time scales.

4 PUBLICATIONS

This cumulative thesis includes nine publications as listed below. In addition, my contribution to each study is explained.

Publication I

Thatje, S., 2003.

Campylonotus arntzianus, a new species of the Campylonotidae (Crustacea: Decapoda: Caridea) from the Scotia Sea (Antarctica)

Polar Biology 26: 242-248

I did the sampling, taxonomic work as well as writing the manuscript.

Publication II

Thatje, S., Bacardit, R., 2000.

Morphological variability in larval stages of *Nauticaris magellanica* (A. Milne Edwards, 1891) (Decapoda: Caridea: Hippolytidae) from South American waters.

Bulletin of Marine Science 66 (2): 375-398

Plankton sampling in the south-western Atlantic Ocean and sorting of the samples was done by the second author. Analyses of the larval developmental stages and drawings were performed by both authors. I developed the concept of this work and did the data interpretation and writing of the manuscript.

Publication III

Thatje, S., Bacardit, R., Romero, M.C., Tapella, F., Lovrich, G.A., 2001.

Description and key to the zoeal stages of the Campylonotidae (Decapoda, Caridea) from the Magellan Region.

Journal of Crustacean Biology 21 (2): 492-505

Sampling was performed by all authors during different campaigns. Larval analyses and taxonomic work was done in joint cooperation between the first and the second author. I developed the concept of this work and wrote the manuscript.

Publication IV

Thatje, S., Lovrich, G.A., Anger, K., 2004.

Egg production, hatching rates, and abbreviated larval development of *Campylonotus vagans* Bate, 1888 (Crustacea: Decapoda: Caridea) in subantarctic waters.

Journal of Experimental Marine Biology and Ecology 301: 15-27.

I developed the idea of this study and did the sampling. The laboratory work and processing of data was done in joint cooperation with the second author. I wrote the manuscript. The final version was achieved considering the revisions by both co-authors.

Publication V

Thatje, S., Lovrich, G.A., Torres, G., Hagen, W., Anger, K., 2004.

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

Journal of Experimental Marine Biology and Ecology 301: 159-174.

The laboratory work and developing the scientific idea was done in joint cooperation with the second author. I was introduced into the lipid and fatty acid analyses in the lab of W. Hagen; protein analyses was performed in joint cooperation with G. Torres; elemental analyses was done in cooperation with K. Anger. I processed the data and wrote the manuscript. The final version was discussed with all authors.

Publication VI

Thatje, S., Schnack-Schiel, S.B., Arntz, W.E., 2003.

Developmental trade-offs in Subantarctic meroplankton communities and the enigma of low decapod diversity in high southern latitudes.

Marine Ecology Progress Series 260: 195-207.

I developed the scientific idea, sorted most of the plankton samples and did all larval identification. I also did all data processing and manuscript writing; the manuscript was improved in cooperation with the co-authors.

Publication VII

Lovrich, G.A., **Thatje, S.**, Calcagno, J.A., Anger, K., Kaffenberger, A., 2003.
Changes in biomass and chemical composition during lecithotrophic larval development of the Southern king crab *Lithodes santolla* (Molina).
Journal of Experimental Marine Biology and Ecology 288: 65-79

Rearing of larvae and sampling was done by all authors. I participated in developing the scientific idea, data treatment and did great part of the manuscript writing. The final version was achieved in joint cooperation of all authors.

Publication VIII

Anger, K., **Thatje, S.**, Lovrich, G.A., Calcagno, J.A., 2003.
Larval and early juvenile development of *Paralomis granulosa* reared at different temperatures: tolerance of cold and food limitation in a lithodid crab from high latitudes.
Marine Ecology Progress Series 253: 243-251.

I developed the scientific idea with the first author. The transport of life animals to Germany was mainly done by myself; rearing of larvae and sampling was performed by all authors. The first author wrote the manuscript and the final version was achieved considering the suggestions by all authors.

Publication IX

Thatje, S., Fuentes, V., 2003. First record of anomuran and brachyuran larvae (Crustacea: Decapoda) from Antarctic waters.
Polar Biology 26: 279-282

Field sampling was performed by the second author. I developed the scientific idea, did all taxonomic work and wrote the manuscript.

Polar Biol (2003) 26: 242–248
DOI 10.1007/s00300-002-0469-5

ORIGINAL PAPER

Sven Thatje

Campylonotus arntzianus, a new species of the Campylonotidae (Crustacea: Decapoda: Caridea) from the Scotia Sea (Antarctica)

Received: 7 August 2002 / Accepted: 24 November 2002 / Published online: 7 February 2003

Abstract Two specimens of *Campylonotus arntzianus* sp. nov. were caught in the Antarctic Scotia Sea off Saunders Island (57°40.31'S, 26°27.81'W) using an Agassiz trawl at one station (depth: 475–589 m). The new species described here is the fifth representative of the monogeneric family Campylonotidae, and the first of the family south of the Antarctic Convergence. *Campylonotus arntzianus* sp. nov. is a shrimp of about 5 cm in total length. Due to similarities in adult morphology, *C. arntzianus* sp. nov. seems to be closely related to *C. capensis*, a deep-sea species from the Southern Atlantic Ocean. A simple key for the species identification of the Campylonotidae is provided.

Introduction

The family Campylonotidae Sollaud, 1913, was originally divided into the two genera *Campylonotus* Bate, 1888 and *Bathypalaemonella* Balss, 1914, the latter comprising a few members of deep-sea species (e.g. Bruce 1966; Pequegnat 1970; Wicksten and Méndez 1983). Due to an increasing number of new species with different morphological characters in the genus *Bathypalaemonella*, de Saint-Laurent (1985) transferred this genus from the Campylonotidae to the Bathypalaemonellidae. Recently, this family was divided into two genera (Cleva 2001).

Members of the genus *Campylonotus* are shallow sublittoral to deep-sea species, predominantly assigned to Subantarctic regions of the southern hemisphere (Thatje et al. 2001). *Campylonotus vagans* Bate, 1888, has been recorded from the southeastern Pacific on the Chilean coast (about 41–56°S) by Retamal (1981), Gorny (1999), Thatje et al. (2001), and from the Argentine sector of the Southern Atlantic (Torti and Boschi 1973; Boschi et al. 1992), extending north to the latitude of Buenos Aires (about 35°S). That species was found from the shallow sublittoral down to about 300 m water depth. *Campylonotus semistriatus* Bate, 1888, seems to be exclusively restricted to the channel and fjord system of the Strait of Magellan and Tierra del Fuego at water depths of 150–500 m (Retamal 1981; Boschi et al. 1992; Thatje et al. 2001). The third species from the Atlantic sector, *C. capensis* Bate, 1888, is mainly known to occur as deep-sea shrimp along the continental platform of the Argentine Atlantic shelf north to the continental slope off Brazil, at depths ranging from 700 to 1,300 m (Boschi et al. 1992; Spivak 1997; Gorny 1999). However, this species was also found in shallower waters (140 m) at Marion Island (46°43'S, 38°4'30"E; Bate 1888; Yaldwyn 1960), which may indicate a more circumpolar distribution of the species. The only Indopacific representative of this genus is *C. rathbunae* Schmitt, 1926, which has been found in the Great Australian Bight and off the east coast of New Zealand at depths of 155–800 m (Yaldwyn 1960; Pike and Williamson 1966).

There is generally little knowledge of the life history of the Campylonotidae. Protandrous hermaphroditism is assumed for all four previously assigned campylonotid species (Yaldwyn 1960, 1966; Torti and Boschi 1973; Thatje and Lovrich 2003) and seems to be a pattern typical to the family (Yaldwyn 1960). These species seem to follow an abbreviated larval development, passing through a minimum of two zoeal stages and one decapodid stage (Pike and Williamson 1966; Thatje et al. 2001). This abbreviated development is already indicated by well-developed zoea I (for discussion, see Pike and Williamson 1966), but was only completely followed in laboratory cultures of larvae of *C. vagans* (Thatje and Lovrich 2003). Although, from an evolutionary point of view, first larvae are quite advanced in development, with respect to the complete palp divisions of the maxilla and the maxillule and the large pereiopodal exopods, it is among the most primitive caridean larvae (Pike and Williamson 1966; Thatje et al. 2001). Its systematic position on the basis of larval characteristics resulted in

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controversial discussion (see Borradaile 1907; Balss 1957; Pike and Williamson 1966; Thatje et al. 2001).

The present work gives a detailed description of a new representative of the Campylonotidae, *C. arntzianus* sp. nov. from waters off Saunders Island (South Sandwich Islands), and that is the first representative of the Campylonotidae for Antarctic waters.

Materials and methods

Two specimens of the new species were obtained from an Agassiz trawl (sampling depths: 475–589 m) at one station off Saunders Island (South Sandwich Islands, 57°40.31'S, 26°27.81'W, Fig. 1) during the "Latinamerican Polarstern Study" (LAMPOS, ANT XIX/5, April 2002). Both specimens were photographed in order to record coloration previous to fixation. The specimens were fixed in 4% buffered formalin and later transferred into 70% ethanol. The paratype was dissected in the laboratory, and appendages and mouthparts drawn using a Zeiss stereomicroscope. The type material is deposited in the Crustacea collection of the Zoological Museum of the Humboldt University, Berlin, Germany.

Results

Systematics

Order	Decapoda Latreille,	1803
Suborder	Dendrobranchiata Bate,	1888
Superfamily	Palaemonoidea Rafinesque,	1815
Family	Campylonotidae Sollaud,	1913

Diagnosis

Genus *Campylonotus* Bate, 1888: first pair of pereiopods chelate, with only one movable finger; second pair of pereiopods equal; pereiopods without exopods; arthrobranchs and epipods at bases of first four pairs of pereiopods. Upper antennal flagellum simple. Basal part of rostrum with not more than five teeth, the first of which stands behind the middle of carapace (changed after Holthuis 1952, 1955; see also Yaldwyn 1960; Torti and Boschi 1973).

Campylonotus arntzianus, new species

Material examined Saunders Island (South Sandwich Islands, Scotia Sea, Antarctica). PFS Polarstern expedition "LAMPOS, ANT XIX/5"; sampling location, station no. PS61/207, 57°40.31'S, 26°27.81'W, 16 April 2002 (Fig. 1). AGT sampling depth, 475–589 m. Two male specimens of *Campylotonus arntzianus* sp. nov., holotype, CL = 11.1 mm, TL = 53.7 mm; paratype, CL = 10.3 mm, TL = 53.2 mm. Zoological Museum of the Humboldt University, Berlin, Germany (reg. no. ZMB 27453) (Figs. 2, 3, 4).

Etymology The species is named after Prof. Dr. Wolf E. Arntz.

Diagnosis A robust prawn of medium size with prominent, blade-like rostrum slightly curved; rostral formula 6/4 (rostral tip with 1 subapical tooth). Telson armed with one mesial tooth and three pairs of spines on posterior margin; six pairs of spines at distal third of surface near lateral margin.

Description Rostrum blade-like and slightly curved; rostral formula known is 6/4, 3 of upper teeth on rostrum proper and 2 posterior of orbit; rostral tip with 1 subapical tooth. Lower margin of rostrum with four pronounced teeth (Fig. 2).

Eyes black, round, corneas not reaching end of first segment of antennular peduncle (Fig. 2).

Carapace smooth, cylindrical, with anterolateral margin rounded. Carapace with branchiostegal and pterygostomian spines (Fig. 2B).

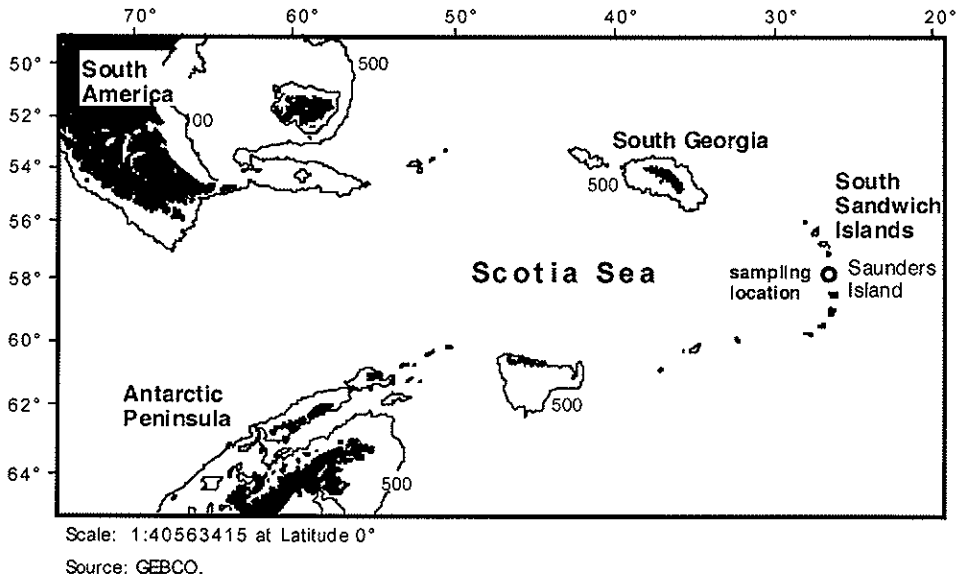

Fig. 1 Sampling location of *Campylonotus arntzianus* sp. nov. from the Scotia Sea, South Sandwich Islands, Antarctica (57°40.31'S, 26°27.81'W). Specimens were caught during the "Latinamerican Polarstern Study" (LAMPOS) in April 2002

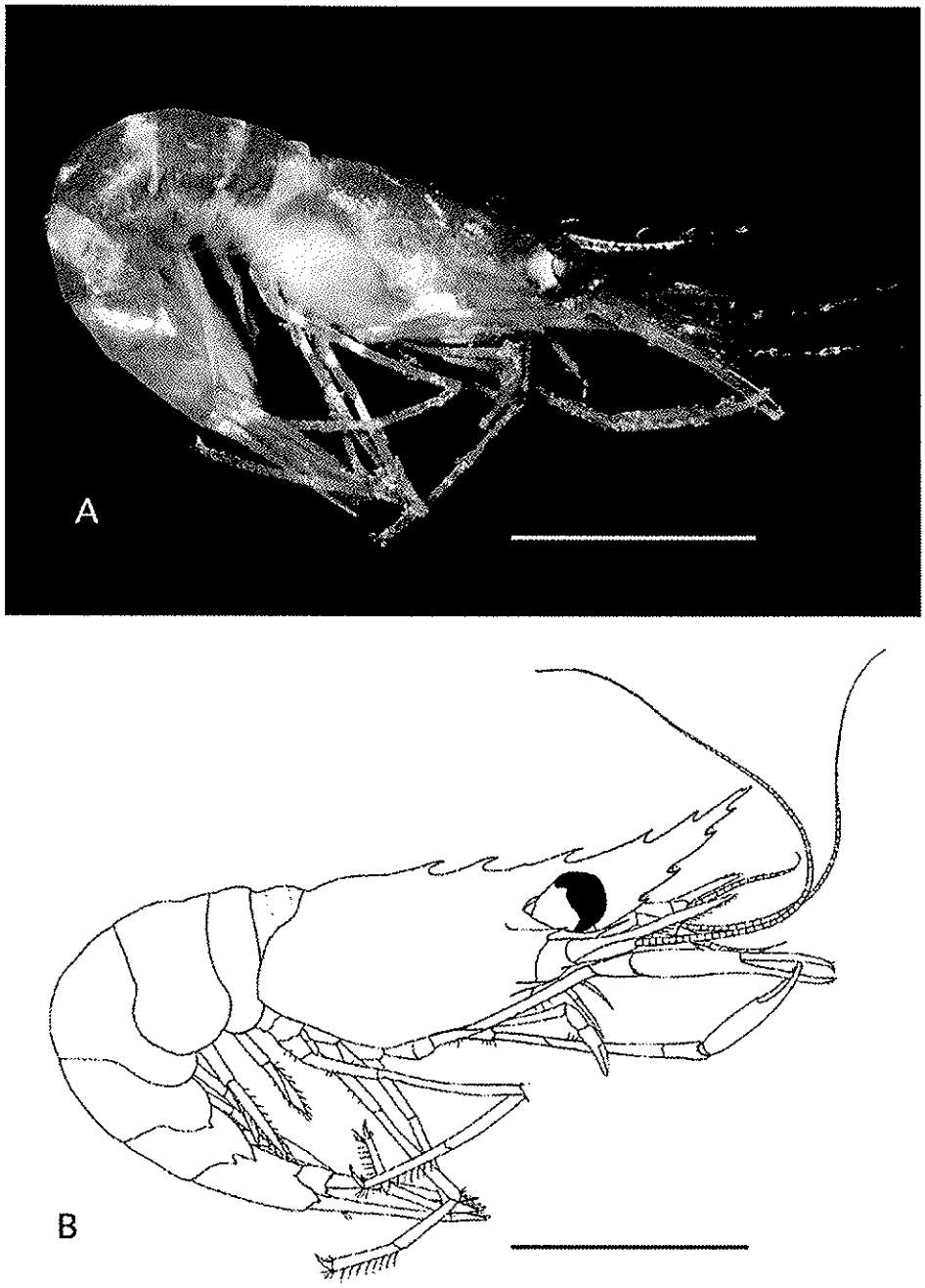

Fig. 2A, B *Campylonotus arntzianus* sp. nov. (ZMB 27453), holotype, male. **A** living holotype, lateral view; photograph by Martin Rauschert. **B** drawing. Scales = 1 cm

Antennular peduncle with slender first segment bearing long, tapering stylocerite, and widely expanded base. Stylocerite reaching about midway along second antennular peduncle, rather broad at base, narrowing gradually to sharp point. Third segment about two-thirds of second, both together about two-thirds of first (Fig. 3A). Outer flagellum of more than 20 segments; inner flagellum about half as long as outer. Inner margin of antennule with dense row of feathered setae, first antennular segment with row of 12 setae at outer margin (Fig. 3A).

Antennal scaphocerite about 3 times as long as broad (Fig. 3B), with straight lateral margin terminating in a strong tooth, which does not project beyond the rounded apex of the lamella. Inner margin with dense row of long feathered setae. Flagellum about twice as long as CL, first three segments broader. Inner margin of antennal basis terminating in a rounded hook.

Mandible with incisor and molar processes fused into one denticulate plate bearing strong cutting edge (Fig. 3C), palp absent.

Maxillule with proximal and distal endites armed with stout bristles (Fig. 3D). Endopod with long aesthetasc on inner apex; endopod bearing second apex at lateral third, with terminal feathered projecting setae;

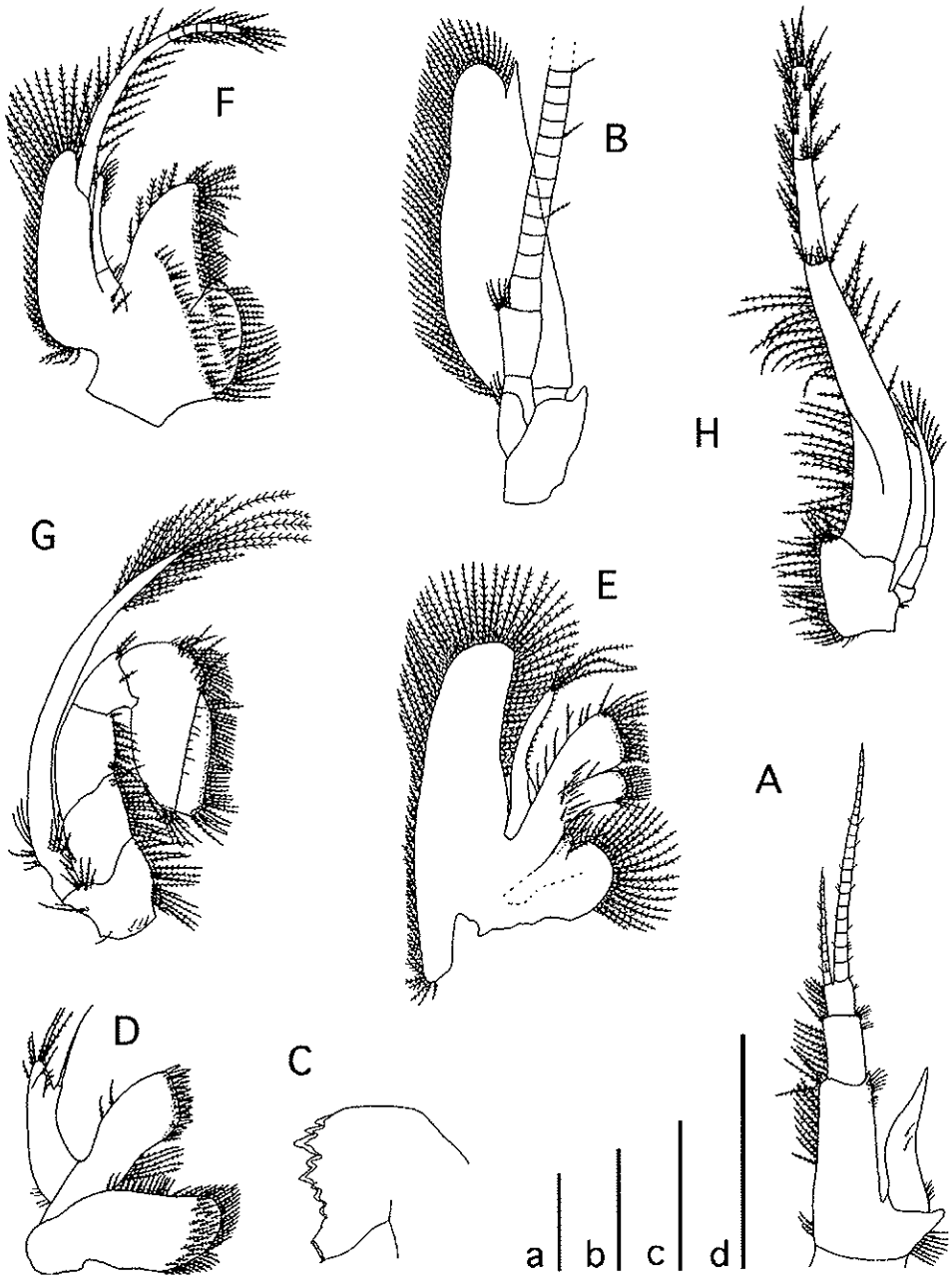

Fig. 3A–H *Campylonotus arntzianus* sp. nov. (ZMB 27453), paratype, male, right side. **A** antennule; **B** antenna; **C** mandible; **D** maxillule; **E** maxilla; **F** maxilliped 1; **G** maxilliped 2; **H** maxilliped 3. Scale bars $a = 2$ mm (**A**, **B**); $b = 2$ mm (**H**); $c = 1$ mm (**C**); $d = 2$ mm (**D–G**)

endopod ending in round apex with row of single feathered setae.

Maxilla with proximal endite unequally bilobed, armed with 65–70 and 7 feathered setae, respectively (Fig. 3E); distal endite well developed and strongly bilobed, together with more than 40 feathered setae. Endopod simple, with four long, slender, feathered apical setae. Scaphognathite large and fringed with feathered setae decreasing in length towards posterior lobe.

Maxilliped 1 with clearly separated proximal and distal endites (Fig. 3F); margins and surface of endites with dense cover of stout bristles; endopod bi-segmented, with apical tuft of setae; exopod with long palp (apical tip of five segments) and large caridean lobe fringed with long, feathered setae.

Maxilliped 2 with well-developed exopod separated from basis. Ischium, merus and carpus separated (Fig. 3G).

Maxilliped 3 with three-segmented exopod, of which first and second segments form a broad basis (Fig. 3H); exopod about half as long as ischium. Endopod of four segments ending in a short apical spine; internal margin with dense row of feathered setae.

Pereiopod 1 chelate (Fig. 4A). Dactylus slightly longer than half length of propodus; fingers of chela (especially tip) setose. Merus about twice as long as

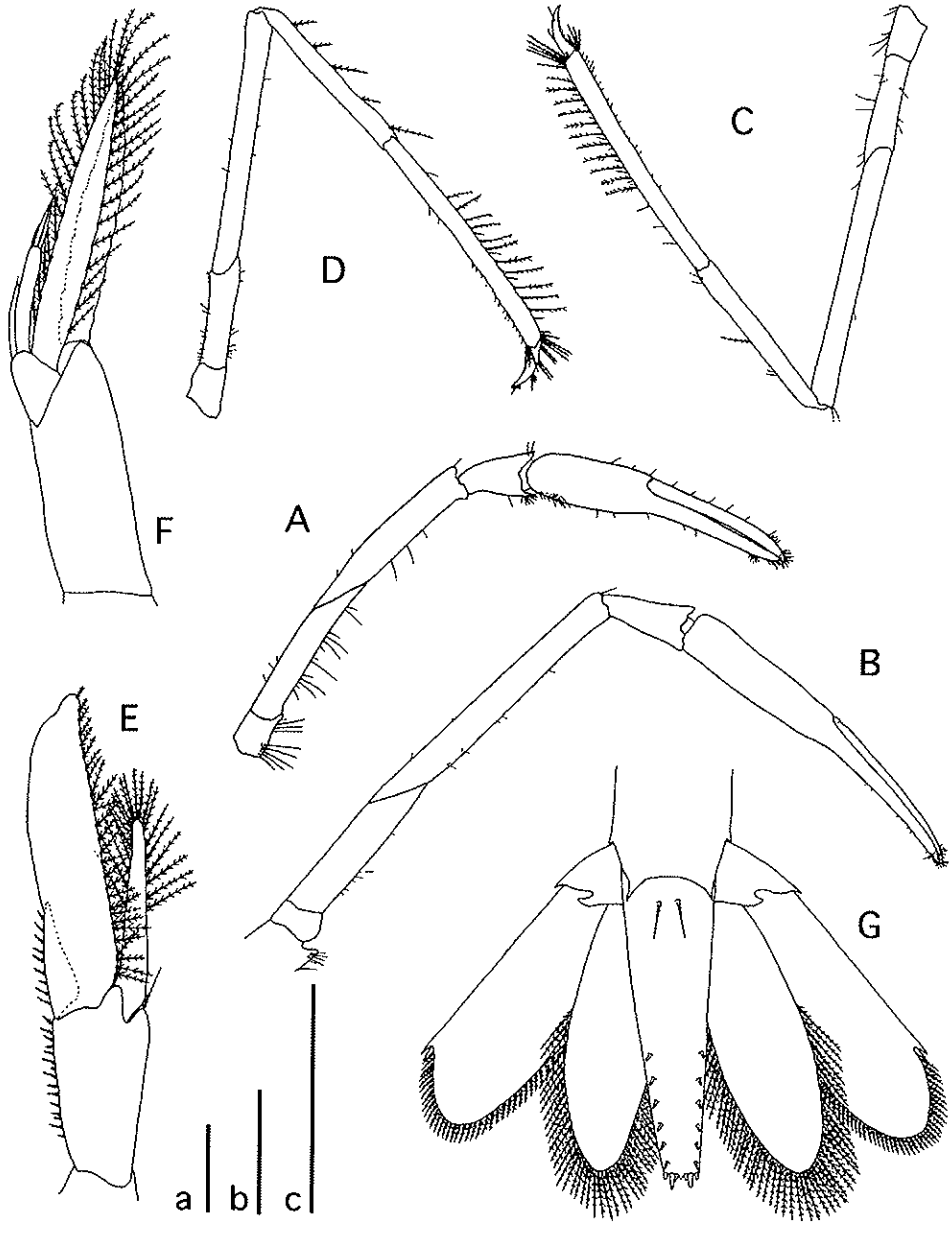

Fig. 4A–G *Campylonotus arntzianus* sp. nov. (ZMB 27453) paratype, male, right side. **A** pereiopod 1, lateral view; **B** pereiopod 2, lateral view; **C** pereiopod 3, lateral view; **D** pereiopod 4, lateral view; **E** pleopod 1, lateral view; **F** pleopod 2, lateral view; **G** telson and uropods, dorsal view. Scale bars: *a* = 1 mm (**A**); *b* = 2 mm (**B–D, G**); *c* = 2 mm (**E, F**)

carpus, 1.2 times ischium; basis short, with two tufts of setae.

Pereiopod 2 chelate (Fig. 4B), almost twice as long as pereiopod 1. Dactylus slightly longer than half length of propodus; fingers of chela (especially tip) setose; propodus now with broader base. Merus about 3 times as long as carpus, twice as long as ischium; basis without setation.

Pereiopods 3–5 almost the same (Fig. 4C, D). Dactylus about one-quarter to one-fifth length of propodus and curves to terminate in a single, acute tip; the concave ventral surface bears several short acute bristles, brush-like; dorsal surface with several feathered setae in pereiopods 4 and 5 (Fig. 4D), pereiopod 3 with two to three spiny setae (Fig. 4C). Propodus and merus about 1.5 times as long as carpus; carpus about 1.5 times as long as ischium. All segments are scarcely covered with short, thin setae. Merus in pereiopod 5 with terminal spine (Fig. 2B).

First pleopod with broad endopod, 4 times as long as broad, 1.7 times as long as exopod, terminating in apical lobe (Fig. 4E); internal margin of basis and first third of endopod with row of short feathered setae; straight-edged exopod tapering to acute tip; exopod fringed with about 20 long, feathered setae.

Second male pleopod with both endopod and exopod with weakly convex setose lateral and medial margins tapering to acute distal tips (Fig. 4F). Basis of endopod slightly expanded, bearing the appendix interna and masculina, 1.7 times as long the appendix interna; appendix masculina with three strong terminal aesthetascs.

Pleurae of somites 1–5 rounded and expanded (Fig. 2B); pleura of somite 3 with small posteriorly directing tooth; posterior margin of the pleura of somite 5 with sharp tooth some distance above the sharply pointed apex. Somite 6 without expansion but pointed apex.

Uropods with endopod about as long as tail fan, exopod slightly longer (Fig. 4G). Exopod with straight lateral margin terminating in strong tooth. Both posterior margins of endopod end exopod with long, feathered setae; exopod with one additional lateral outer spine (Fig. 4G). Telson with straight lateral margins, narrowing posteriorly; posterior margin with mesial tooth and three pairs of apically rounded spines; lateral margins with six pairs of dorsal spines at distal third; telson dorsally with one pair of mesial, posteriorly projecting spines on first quarter; three to five mesial spines ventrally at distal third of telson (not indicated in drawing, Fig. 4G).

Colour Living specimens were of bright, dark-orange-red. Lateral sides of carapace changed to greyish-white; pereiopods irregularly striped white; somites with diffuse white stripes dispersing towards posterior margins. Both specimens obtained showed variable colouration, which I assume to be a general pattern in this species, as known from other Campylonotidae.

Discussion

Taxonomic remarks

Campylotonus arntzianus sp. nov. is closely related to *C. capensis*, but can undoubtedly be distinguished on the basis of morphological differences (compare with Bate 1888; Yaldwyn 1960; Torti and Boschi 1973). The main morphological characteristics separating both species are now listed (features of *C. capensis* in parentheses): rostrum slightly curved (strongly curved), with short bristles at basis of ventral teeth (without bristles); carapace without posterior tubercle (tubercle present); somite 4 with pleural tooth (absent); mandible without palp (with two-segmented palp); maxillipeds 1 and 2 without epipod (large epipod and podobranch present). The absence of the mandibular palp and the truncated scaphognathite in *C. arntzianus* sp. nov., which is tapering in all other campylonotid species, might be an indication of a different feeding mode.

General remarks

The benthic decapod fauna of the Antarctic is represented by only about ten natant species (Yaldwyn 1965; Kirkwood 1984; Tiefenbacher 1990), but these often occur in large concentrations and great biomass on the high-Antarctic shelf. Little is known of the decapod fauna south of the Antarctic Convergence or in the shallows along the Scotia Arc. The latter are assumed to serve as evolutionary footsteps between the Subantarctic Magellan Province of South America and the Antarctic Peninsula. *Campylonotus* was previously recorded as being exclusively Subantarctic, although Gorny (1999, Table 2) cited the occurrence of *C. vagans* on the Antarctic Shelf. I could not discover this Antarctic find during the re-examination of the literature cited in his work (Gorny 1999), and therefore assume it to be a mistake, or probably a confusion of the station data published by Holthuis (1952).

Decapod diversity in the Sandwich Islands area was low and completely different in species composition compared to stations obtained along the northern and southern branch of the Scotia Arc (Romero et al. 2003). In terms of community analyses, Ramos (1999) found a similar benthic faunal pattern as represented by poorly structured communities, including the absence of important suspension-feeder communities typical of the high Antarctic. Ramos (1999) assumed this indication to be due to active volcanism in this area (see also Acosta et al. 1989) serving as continuous disturbance. This find, however, can be confirmed by my own observations during the present scientific cruise to the area: sediments consist of lava and/or soft pumice stone, and no sponge or dense suspension-feeder communities were found at all. In addition to the present new species, two further caridean morphotypes were obtained from this area which have not yet been assigned to known taxa. This indicates that the natant decapod fauna is probably much higher in diversity in the Antarctic than previously assumed.

Campylonotus arntzianus sp. nov. is morphologically closely related to *C. capensis*, a deep-sea shrimp from the southern Atlantic. It is possible that colonisation of the Antarctic by decapod crustaceans is predominantly via the deep sea, where ecological conditions, such as low temperatures and food availability, are in some aspects

Key to species of *Campylonotus* Bate, 1888

– Abdomen dorsally armed with spines and a blunt tubercle	*C. rathbunae* Schmitt, 1926
– Abdomen dorsally unarmed	1
1. Rostrum with 3–4 ventral teeth	2
– Rostrum with more than 4, normally 6–10, ventral teeth	*C. vagans* Bate, 1888
2. One subdorsal rostral spine present	3
– No subdorsal rostral spine	*C. semistriatus* Bate, 1888
3. Rostrum slightly curved, projecting, with short bristles at basis of ventral teeth; carapace without posterior tubercle, somite 4 with pleural tooth	*C. arntzianus* Thatje, 2003
– Rostrum strongly curved, without bristles; carapace with posterior tubercle, somite 4 without pleural tooth	*C. capensis* Bate, 1888

comparable to the Antarctic regime. Adaptation in the reproductive cycle, which I assume to be a clue for survival in polar areas, is often comparable, and might therefore be one key factor for successful colonisation of this area. The same evolutionary pathway has been already suggested for *Chorismus tuberculatus* (Thatje and Bacardit 2000), a deep-water caridean from the southern Atlantic Ocean.

Acknowledgements This paper is dedicated to Professor Dr. Wolf Arntz (Alfred Wegener Institute, Germany) on the occasion of his 60th birthday. In addition to his extensive research on Antarctic decapods and invertebrate communities in general, he encouraged my own interest in this subject and greatly supported my scientific work. I am indebted to Dr. Martin Boche and his crew of the German PFS *Polarstern* for help and assistance at sea, and to Dr. Gustavo Lovrich, M. Carolina Romero, Federico Tapella and Fabian Vanella for the excellent working atmosphere and fruitful research during this cruise. Dr. Martin Rauschert kindly provided the holotype photograph published in this work. I am grateful to Dr. Pablo J. López-Gonzalez and two anonymous reviewers for their helpful comments on the manuscript. I would like to thank Ruth Alheit for her revision of the English.

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BULLETIN OF MARINE SCIENCE, 66(2): 375–398, 2000

MORPHOLOGICAL VARIABILITY IN LARVAL STAGES OF *NAUTICARIS MAGELLANICA* (A. MILNE EDWARDS, 1891) (DECAPODA: CARIDEA: HIPPOLYTIDAE) FROM SOUTH AMERICAN WATERS

Sven Thatje and Rosa Bacardit

ABSTRACT

Of the three species of hippolytid shrimps known to occur in the southwestern Atlantic Ocean, *Nauticaris magellanica* (A. Milne Edwards, 1891) is the only representative of its genus. Zoeal larvae of *N. magellanica* were obtained from plankton samples taken by means of a plankton net in Argentine waters in the southwestern Atlantic Ocean during two expeditions carried out from onboard the RV Walther Herwig and the RV Shinkai Maru in 1978 and 1979, respectively. In the present work we distinguish and redescribe six zoeal stages of *N. magellanica* and compare our results with the previous description of larvae reared under laboratory conditions from a population off central southern Chile. Differences in size, number of setae on the appendages as well as in the development of the pereiopods are discussed from an ecological and biogeographical point of view.

The general knowledge of meroplanktonic larvae and their ecology is still limited, and taxonomists mainly focus on larval descriptions in order to facilitate studies on plankton ecology (e.g., Wehrtmann and Báez, 1997). However, due to the lack of larval descriptions it is hardly possible to work on a species level with decapod larvae. This is especially true for species inhabiting South American waters. Rearing larvae obtained from ovigerous females is the main method for analyses of larval development and allows a clear identification at the species level. In the history of larval research it has frequently been shown that larvae reared in the laboratory, and especially carideans, show a great variability in larval stages and morphology (Knowlton, 1974; Sandifer and Smith, 1979; Boschi, 1981; Criales and Anger, 1986; Wehrtmann, 1991). Published comparisons between decapod larvae reared in the laboratory and field-collected larvae do not exist, although laboratory observations give evidence that morphological variability might be a common pattern in nature, too. The amount of variability complicates the work of ecologists, and is one reason why scientists working on larval development and ecology mainly focus on autecological studies (e.g., Palma, 1994; Wehrtmann and Albornoz, 1998).

Nauticaris magellanica is the only representative of this genus inhabiting the coastal waters of southern South America (Holthuis, 1952; Méndez, 1981; Boschi et al., 1992). At the Pacific coast this shrimp is known to cover a geographical range of approximately 35° of latitude (Wehrtmann and Kattner, 1998), and therefore it is an ideal species for the study of ecological adaptations to different environmental conditions. It has been recorded from all parts of the Chilean coast (Retamal, 1981), except the South Patagonian Icefield (latitudinal range: 48°20′S to 51°30′S, Aniya and Skvarca, 1992; Mutschke et al., 1996), and is the most abundant shrimp associated with mussel raft cultures and holdfast of the kelp *Macrocystis pyrifera* (Aracena and López, 1973; Ojeda and Santelices, 1984). At the Atlantic coast, *N. magellanica* is known to occur from the coastal waters of Buenos Aires (Argentina) south to the Beagle Channel (Magellan region), as well as around the Falkland Islands/Islas Malvinas (Spivak, 1997; Boschi et al., 1992).

Wehrtmann and Albornoz (1998) provide a complete description of the larval development of *N. magellanica* reared from egg-carrying females obtained from a population collected from mussel raft culture (*Mytilus chilensis*) off central Chile (41°35′50″S, 72°42′53″W). Their work constitutes the first complete description for zoeal development in this genus. In our present study, we compare these larval descriptions with larvae of *N. magellanica* obtained from plankton samples taken in the southwestern Atlantic Ocean (37°35′S to 55°15′S; 53°40′W to 68°15′W), and discuss differences in size and morphology in relation to ecological adaptations and biogeographical separation.

Material and Methods

In the present work we provide information on the larval morphology of the hippolytid decapod *N. magellanica*. The material studied was collected in Argentine waters in the southwestern Atlantic Ocean (37°35′S to 55°15′S; 53°40′W to 68°15′W, see Fig. 1) during two expeditions carried out onboard the RV Walther Herwig and RV Shinkai Maru in 1978 (August to October) and 1979 (January to March), respectively (Ciechomski et al., 1979; Cousseau et al., 1979). Samples were collected by means of a Bongo net of 330 μm mesh size and were preserved in 3% formalin solution buffered with hexamethylenetetramine. Complete descriptions of the cruises and additional information on oceanographic measurements can be obtained from Ciechomski et al. (1979).

Carapace length (CL) was measured from the posterior edge of the orbital arch to the mid-dorsal posterior margin of the carapace; total length (TL) of the larvae was measured from the posterior margin of the orbital arch to the distal margin of the telson, excluding setae. The descriptions of larval stages represent an average of our observations. Nomenclature used for the differentiation of the larval phases and morphology corresponds to that suggested by Williamson (1960, 1968, 1982), Gurney (1942), Boschi (1981), Haynes (1978, 1981, 1985) and Albornoz and Wehrtmann (1997).

We compare our larval descriptions with that of Wehrtmann and Albornoz (1998) who reared larvae of *N. magellanica*, obtained from an adult population of a mussel raft culture (*M. chilensis*) in central southern Chile (41°35′50″S, 72°42′53″W).

Family Hippolytidae
Nauticaris magellanica (A. Milne Edwards, 1891)

Zoea I
TL = 2.2 ± 0.02 mm; CL = 0.6 ± 0.01 mm; n = 12

General Characteristics (Fig. 2A, B).—Eyes sessile; anterior and posterior part of carapace with small protuberances; rostrum acute and lightly curved down; one pair of pterygostomian spines present; supraorbital and antennal spines absent; 2nd abdominal segment without pleura; 6th abdominal segment continuous with telson.

Antennule (Fig. 2J).—Terminal region of external flagellum with three aesthetascs and one simple apical internal seta; internal flagellum with long plumodenticulate seta; protopodite long and without segmentation.

Antenna (Fig. 2K).—Exopodite with nine long plumose setae on internal margin (including tip) and two short external plumose setae; distal region divided in four segments; medium-internal margin of exopodite with small papilla; endopodite approximately two

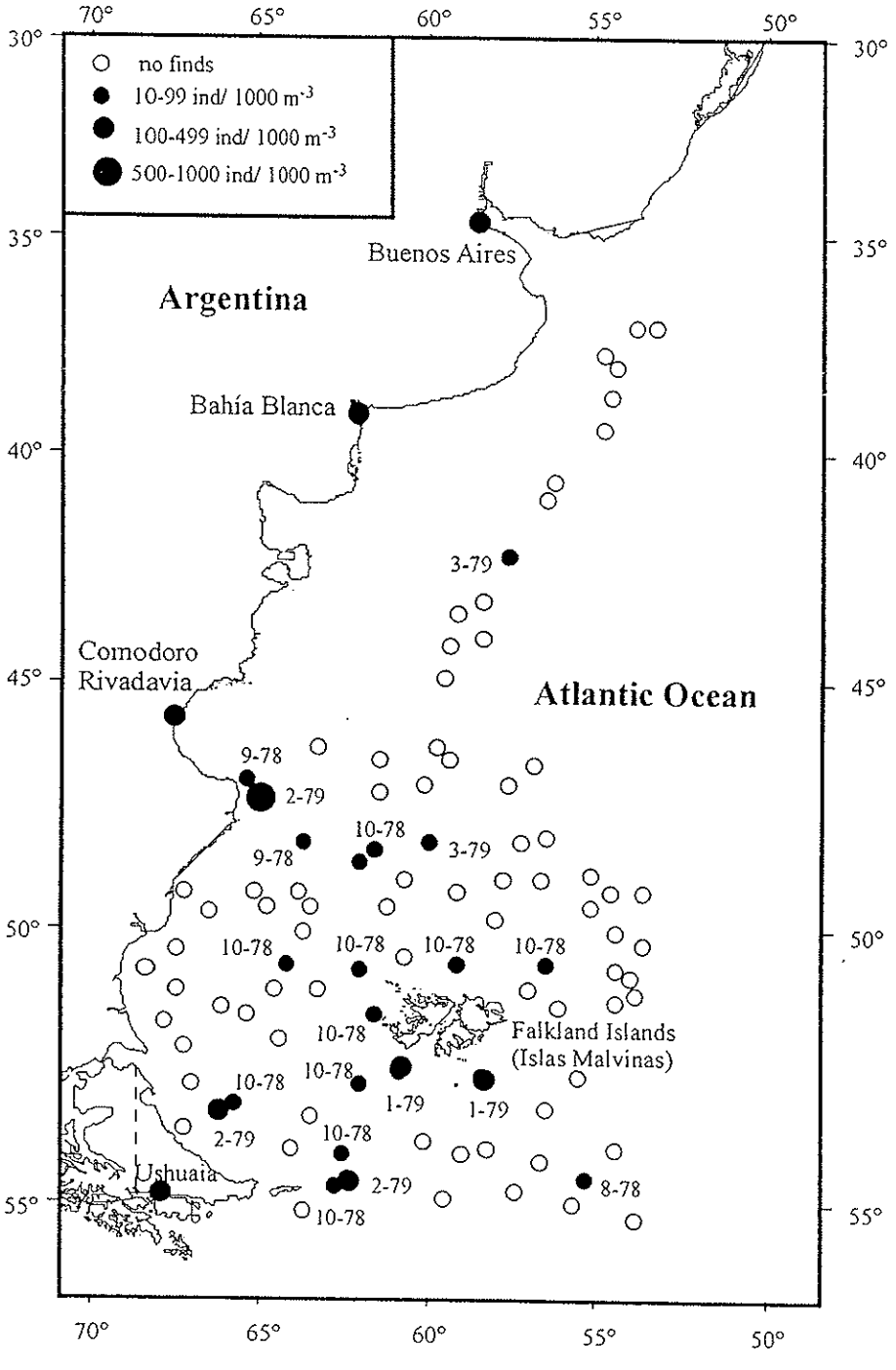

Figure 1. Sampling locations of larvae of *Nauticaris magellanica* in the southwestern Atlantic Ocean (Argentina) carried out onboard the RV WALTHER HERWIG and the RV SHINKAI MARU from August 1978 to March 1979 (sampling month and year as indicated by the numbers).

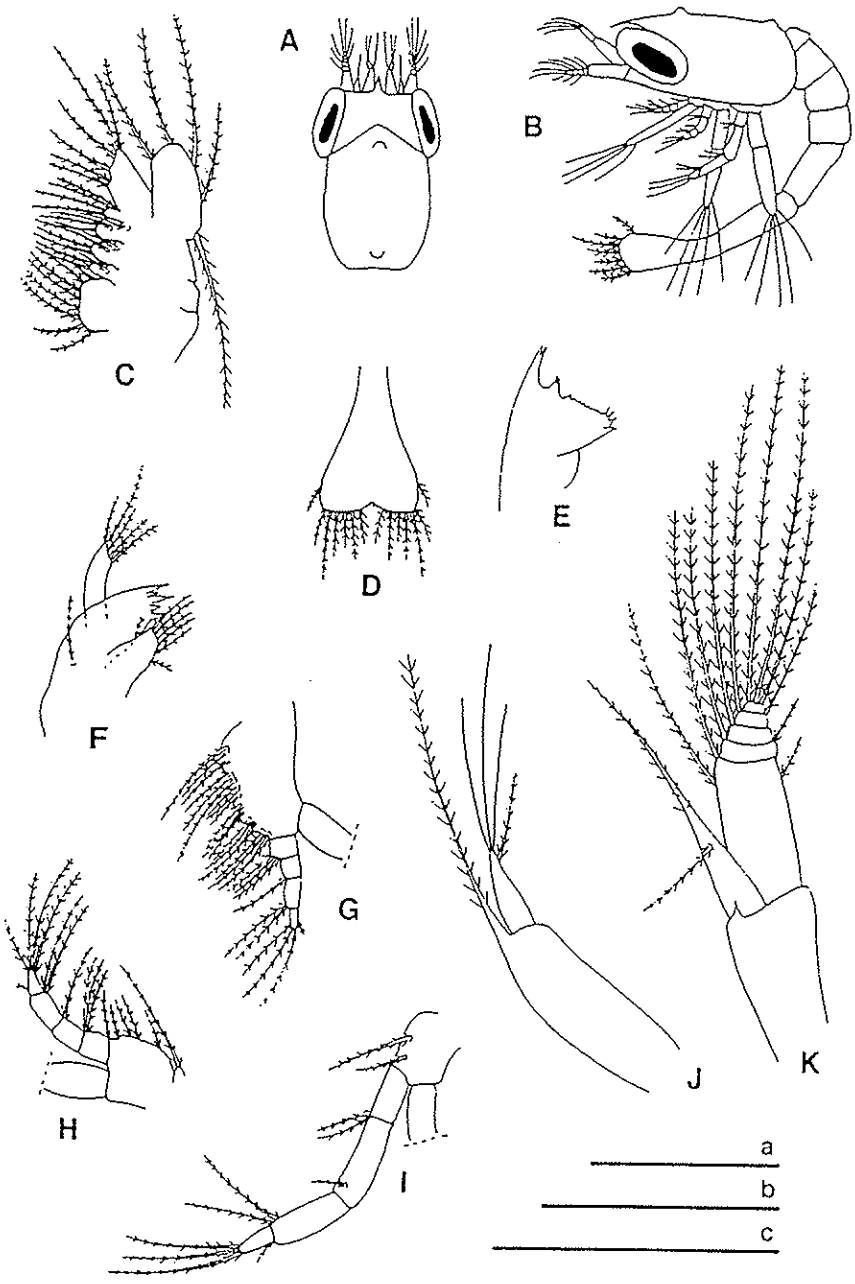

Figure 2. Zoea I. A: carapace with cephalic appendages, dorsal view; B: lateral view; C: maxilla; D: telson; E: mandible; F: maxillule; G: maxilliped I; H: maxilliped II; I: maxilliped III; J: antennule; K: antenna. Scale bars: a = 0.2 mm (C, E–F, J–K); b = 1 mm (A–B, D); c = 0.5 mm (G-I).

times larger than exopodite; with long plumose seta in medial position, distally bearing numerous denticles; protopodite with one small spine located on base of endopodite.

Mandible (Fig. 2E).—Incisor and molar processes present; incisor process bearing two strong terminal denticles; molar process with denticles and one protuberance.

Maxillule (Fig. 2F).—Endopodite with three plumodenticulate terminal setae and 12 subterminal setae; coxal endite with two long plumodenticulate and two short setae on lateral margin of endite, and three cuspidate setae on its distal part; internal margin with row of short, simple setae (microtrichia); basal endite with three spiniform setae, 2–3 spines with denticles and one serrate seta; protopodite with one plumose seta.

Maxilla (Fig. 2C).—Endopodite bilobed, with distal lobe longer, presenting 2, 1, 1, 2 plumodenticulate setae, from proximal to distal; proximal lobe with two plumodenticulate and one plumose setae; coxal endite with six plumose and three plumodenticulate setae on proximal lobe, and with two plumodenticulate and two plumose setae on distal lobe; basal endite with three plumodenticulate and one plumose setae on both proximal and distal lobe; scaphognathite with five plumose setae, one of which in apical region; internal margin of both endopodite and scaphognathite with row of small simple setae.

Maxilliped I (Fig. 2G).—Coxopodite with six plumodenticulate setae; basipodite with 3, 3, 3, 3 plumodenticulate setae on internal margin; endopodite of four segments with 3, 1, 2 and 4 proximal and distal setae; exopodite with three plumose natatory terminal setae and 1 subterminal one.

Maxilliped II (Fig. 2H).—Coxopodite with one plumodenticulate seta on internal margin; basipodite with 2, 3, 3 plumodenticulate setae; endopodite of four segments with 3, 1, 2, and 4 proximal and distal setae, respectively, exopodite with three terminal plus two subterminal plumose natatory setae.

Maxilliped III (Fig. 2I).—Coxopodite without setae; basipodite with 1, 1, 2 plumodenticulate setae on internal margin; endopodite composed of four segments: distal one with three terminal and one subterminal setae; exopodite with three terminal and two subterminal plumose natatory setae.

Pereiopods.—Absent.

Abdomen (Fig. 2B).—With 5 segments, 6th segment continuous with telson; pleopods absent.

Uropods.—Absent.

Telson (Fig. 2D).—Subtriangular; with 7+7 spines with external pair located laterally; with pronounced median indentation.

Zoea II

TL = 2.9 ± 0.08 mm; CL = 0.7 ± 0.03 mm; n = 11

General Characteristics (Fig. 3A,B).—Eyes pedunculate; carapace with pair of pterygostomian and supraorbital spines, but lacking antennal spines; rostrum more pronounced and lightly curved down; 6th abdominal somite still continuous with telson.

Antennule (Fig. 3H).—Internal flagellum small and with one long plumodenticulate terminal seta; external flagellum with four aesthetascs and one seta; distal margin of protopodite with two short plumose setae.

Antenna (Fig. 3D).—Exopodite (including tip) with eight long and two short plumose setae; distal tip 4-segmented; internal medial margin of exopodite without papilla.

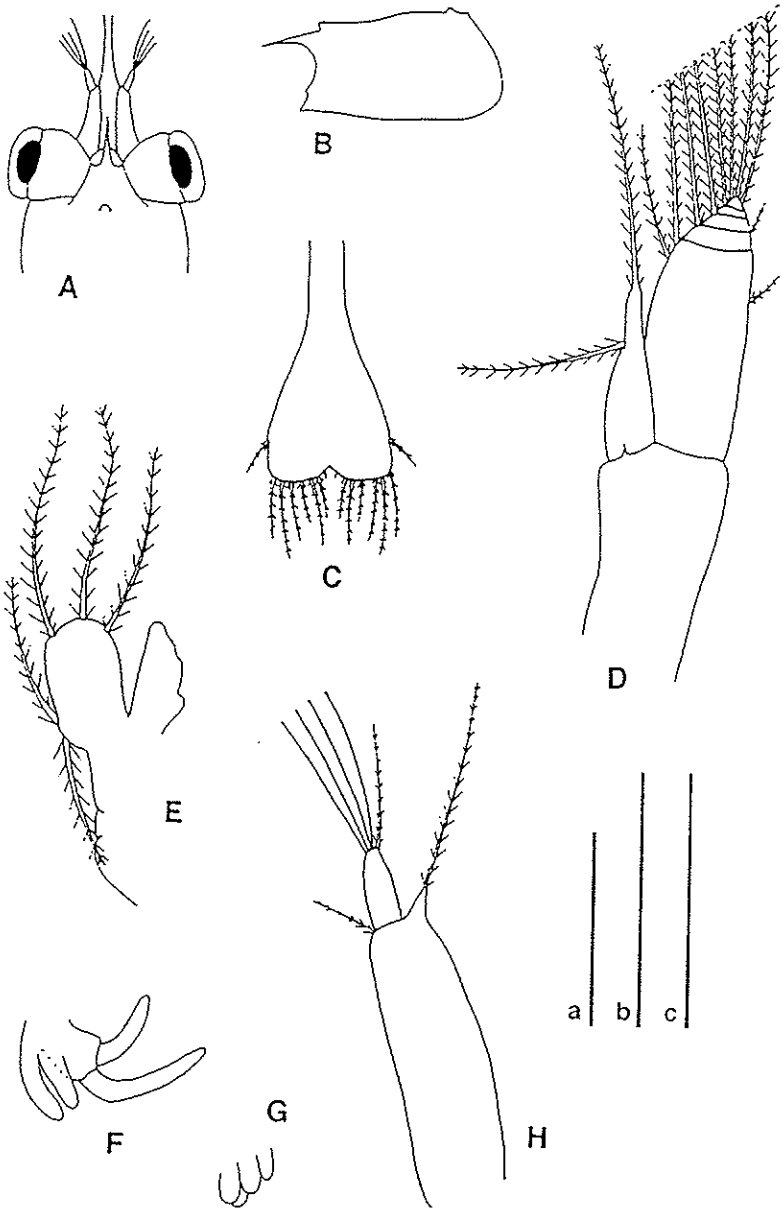

Figure 3. Zoea II. A: anterior part of carapace with cephalic appendages, dorsal view; B: carapace, lateral view; C: telson; D: antenna; E: maxilla; F: pereiopods I - II; G: pereiopods III – V; H: antennule. Scale bars: a = 0.2 mm (D–E, H); b = 1 mm (A–C); c = 0.5 mm (F–G).

Mandible.—Without changes.

Maxillule.—Coxal endite with seven setae; basal endite with five spines and two thinner ones; no other differences to previous stage.

Maxilla (Fig. 3E).—Proximal lobe of coxal endite with 11 plumose and four plumodenticulate setae; distal lobe with 2+2 plumodenticulate and plumose setae, re-

spectively; proximal lobe of basal endite with 3+1 plumodenticulate and plumose setae, respectively; scaphognathite with four subterminal plus one apical plumose setae, one being apical; no other differences to previous stage.

Maxilliped I.—Coxopodite with eight plumodenticulate setae; basipodite with 3, 4, 4 and 3 proximal and distal setae, respectively; exopodite with four terminal and one subterminal plumose setae; no other differences to previous stage.

Maxilliped II.—Coxopodite with one plumodenticulate seta; endopodite 5-segmented, 1st one with one long plumose seta on internal margin, and 5th segment with six simple and serrate setae; exopodite with six plumose natatory setae; no other differences to previous stage.

Maxilliped III.—Coxopodite without setae; endopodite 5-segmented, 5th one with 3+1 setae; exopodite with six plumose natatory setae; no other differences to previous stage.

Pereiopods (Fig. 3F,G).—1st pereiopod biramous, semi-developed; 2nd and 3rd pereiopod biramous, rudimentary; 4th and 5th pereiopod rudimentary, represented by a small bud.

Abdomen.—As in previous stage.

Pleopods.—Absent

Uropods.—Absent.

Telson (Fig. 3C).—Subtriangular; posterior margin with 8+8 processes external pair laterally located, inner pair extremely short.

Zoea III

TL = 3.9 ± 0.12 mm; CL = 1.0 ± 0.08 mm; n = 13

General Characteristics (Fig. 4A,B).—Carapace with one pair of supraorbital, antennal and pterigostomian spines; abdomen divided in six segments plus telson; rostrum slightly curved down.

Antennule (Fig. 4F).—Internal flagellum with one long plumose seta; protopodite 3-segmented; medial segment with two distal external setae; distal segment with one seta at basis of medial lobe; external flagellum with three aesthetascs and one seta.

Antenna (Fig. 4E).—Distal region 2-segmented; external spine well developed, without external setae, internal margin (including tip) with 11 setae; endopodite (including terminal spine) as long as exopodite.

Mandible.—Similar to previous stages.

Maxillule.—Coxal endite with three cuspidate setae, two long plumodenticulate and 2–3 plumodenticulate fine and short setae; basal endite with one spiniform seta, five spines armed with spinules, and two serrate setae; no other differences to previous stage.

Maxilla (Fig. 4D).—Proximal lobe of coxal endite with 13 plumose and four plumodenticulate setae; distal lobe with two plumodenticulate and two plumose setae; proximal and distal lobe of basal endite with four plumodenticulate and one plumose setae, respectively; scaphognathite with 10 subapical plus one apical plumose setae, one being apical.

Maxilliped I.—Basipodite with 3, 4, 4, 4 plumodenticulate setae; coxopodite with eight setae; no other differences to previous stage.

Maxilliped II.—Without changes compared to previous stage.

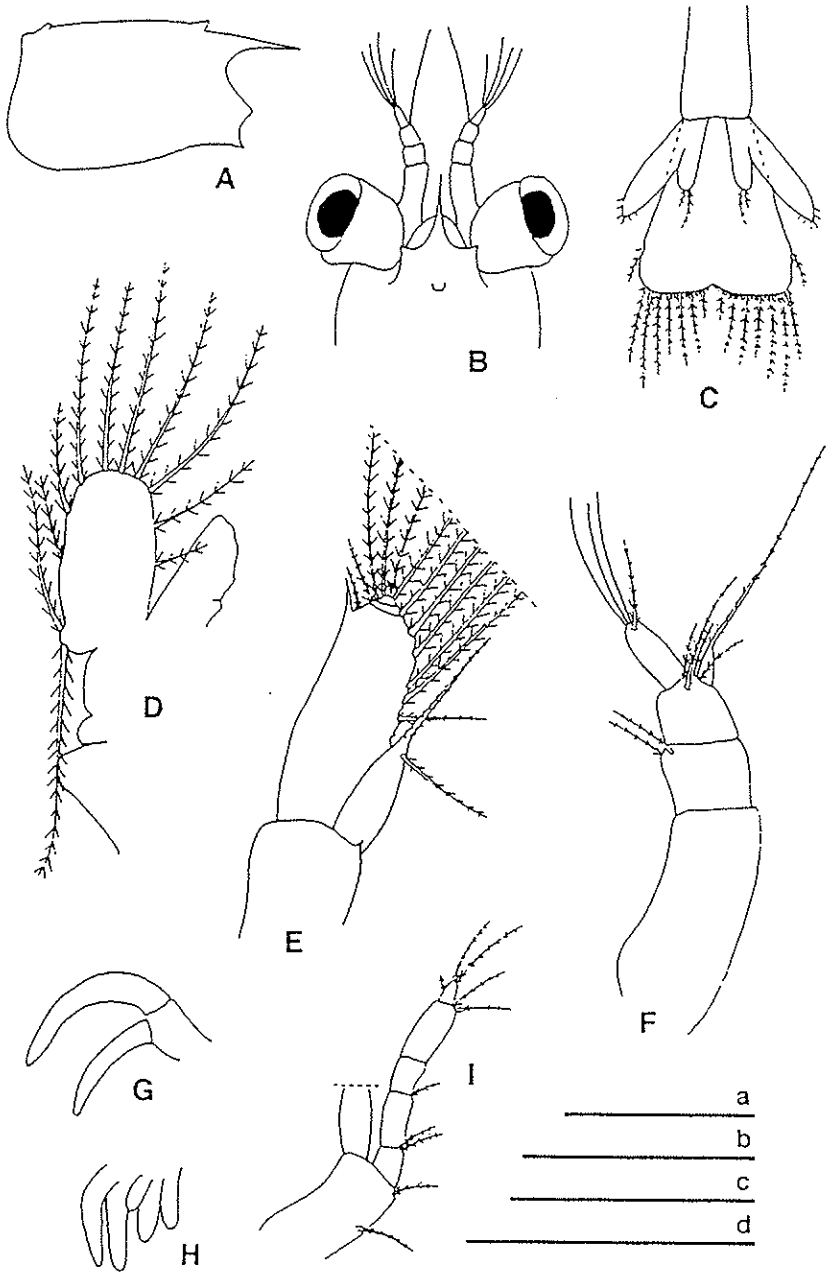

Figure 4. Zoea III. A: carapace, lateral view; B: anterior part of carapace with cephalic appendages; C: uropods and telson; D: maxilla; E: antenna; F: antennule; G: pereiopod II; H: pereiopods III – V; I: pereiopod I. Scale bars: a = 0.2 mm (D); b = 1 mm (A–C); c = 0.5 mm (G–I); d = 0.5 mm (E–F).

Maxilliped III.—Endopodite with 4+1 setae on distal segment; exopodite with eight plumose setae; no other differences to previous stage.

Pereiopods (Fig. 4G,H,I).—First pereiopod completely developed; exopodite with eight plumose natatory setae; basipodite with two setae; endopodite 5-segmented with 2, 1, 0, 2 and 3 proximal and distal setae, respectively, without cheliped; 2nd pereiopod present as biramous buds; pereiopods 3 and 4, biramous, less developed; pereiopods 4 and 5, uniramous, represented as simple buds.

Abdomen.—With 6 segments, 6th segment with one pair of spines on its posterolateral margin.

Pleopods.—Absent.

Uropods (Fig. 4C).—Biramous, developing; exopodite with six short simple setae on its margin, forming tail fan; endopodite with two plumose setae, terminal one three times as long as subterminal one.

Telson (Fig. 4C).—With 8+8 posterior processes, external pair located laterally.

ZOEA IV

TL = 4.03 ± 0.25 mm; CL = 1.03 ± 0.05 mm; n = 16

General Characteristics (Fig. 5A,C).—Eyes pedunculate, laterally oriented; carapace wider than in previous stages; carapace with one pair of supra-orbital, sub-orbital and pterygostomian spines; abdomen 6-segmented, second abdominal segment with developing pleura.

Antennule (Fig. 5D).—Protopodite 3-segmented, stilocerite with three distal setae and two external plumose setae and one internal seta; medial segment with two plumose internal and external setae, respectively; distal segment with one large distal plumodenticulate seta, and one smaller external one; external flagellum with three aesthetascs and one plumose seta; internal flagellum one third the size of external flagellum, with one plumodenticulate seta, as long as external flagellum (including setae).

Antenna (Fig. 5 E).—Endopodite with long plumose setae; endopodite half as long as exopodite; no other differences to previous stage.

Mandible.—Without palp; no other differences to previous stage.

Maxillule.—Coxal endite with nine setae; basal endite with nine spines and one spiniform seta; no other differences to previous stage.

Maxilla (Fig. 5F).—Proximal and distal lobes of coxal endite with 14 and four setae, respectively; basal endites with seven setae, each; scaphognathite with 17 marginal plumose setae, one being apical.

Maxilliped I.—Basipodite with 3, 5, 6, 4 plumodenticulate setae; coxopodite with eight setae; exopodite with six plumose setae; no other differences to previous stage.

Maxilliped II.—Endopodite of five well separated segments; carpus with one external plumose seta; exopodite with six natatory plumose setae; no other differences to previous stage.

Maxilliped III.—Exopodite with eight natatory plumose setae; no other differences from previous stage.

Pereiopod I (Fig. 5G).—Well developed; exopodite with nine natatory plumose setae; caxopodite with two plumose setae; endopodite 5-segmented with 1, 0, 0, one and two plumose setae.

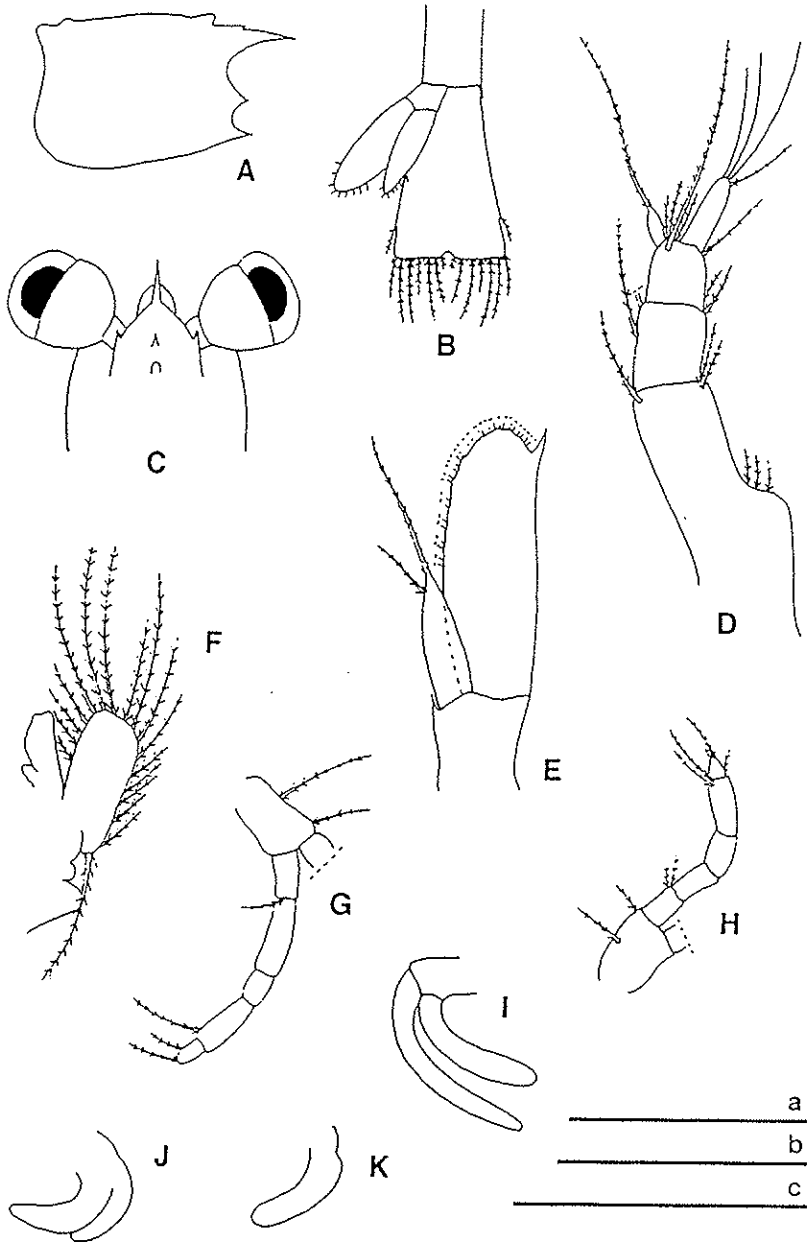

Figure 5. Zoea IV. A: carapace, lateral view; B: uropods and telson; C: anterior part of carapace with cephalic appendages, dorsal view; D: antennule; E: antenna; F: maxilla; G: pereiopod I; H: pereiopod II; I: pereiopod III; J: pereiopod IV; K: pereiopod V. Scale bars: a = 1 mm (A–C); b = 0.5 mm (G–K); c = 0.5 mm (D–F).

Pereiopod II (Fig. 5H).—Developed; exopodite with six natatory plumose setae; coxopodite with two plumose setae; endopodite 5-segmented with 2, 0, 0, 2 and 3 plumose setae.

Pereiopod III (Fig. 5I).—Rudimentary, biramous.

Pereiopod IV (Fig. 5J).—Present as biramous buds.

Pereiopod V (Fig. 5K).—Simple buds.

Pleopods.—Absent.

Uropods (Fig. 5B).—Well developed, biramous; endouropod with seven short marginal setae; exouropod with nine short marginal setae.

Telson (Fig. 5B).—Longer than wide; with 8+8 posterior processes; external pair being located at distal quarter.

ZOEA V

TL = 4.68 ± 0.45 mm; CL = 1.1 ± 0.05 mm; n = 6

General Characteristics (Fig. 6A,B).—Eyes pedunculate; carapace with one pair of dorsal spines on base of rostrum; rostrum generally more pronounced and straight; one pair of suborbital, antennal and pterygostomian spines.

Antennule (Fig. 6E).—Antennal peduncle 3-segmented; stylerocerite with one terminal plumose and 8 plumose setae; basal segment with one internal and six plumose external setae; medial segment with three external and two internal plumose setae; distal medial lobe with four plumodenticulate setae; external flagellum with two subterminal and three terminal aesthetascs and one apical plumose seta.

Antenna (Fig. 6F).—Exopodite with 18 long plumose setae; endopodite half as long as exopodite; lateral setae absent; no other differences to previous stage.

Mandible.—Without palp; no other major differences to previous stage.

Maxillule.—Coxal endite with 13 plumose setae; basal endite with 10 spines and two setae; external seta reduced; no other differences to previous stage.

Maxilla (Fig. 6C).—Proximal lobe of coxal endite with 10 plumose and six plumodenticulate setae; distal lobe with two plumodenticulate and two plumose setae; proximal and distal lobe of basal endite with six and seven plumodenticulate setae, respectively; each one with an additional plumose setae; scaphognathite with 26 marginal setae, one apical and one terminal flagellum.

Maxilliped I.—Coxopodite with eight plumodenticulate setae; basipodite with 4, 5, 5 and 6 plumodenticulate setae; no other differences to previous stage.

Maxilliped II.—Without changes.

Maxilliped III.—Without changes.

Pereiopod I.—Exopodite with 11 natatory plumose setae; endopodite as in previous stage.

Pereiopod II.—Endopodite as in pereiopod I; basipodite with two simple setae; exopodite with 10 natatory plumose setae.

Pereiopod III (Fig. 6G).—Well developed; endopodite 5-segmented with 0, 0, 1, 1, 1 plumose setae; exopodite simple, shorter than endopodite, without setae.

Pereiopod IV (Fig. 6H).—Biramous, rudimentary.

Pereiopod V (Fig. 6I).—Present as simple buds.

Pleopods.—Absent.

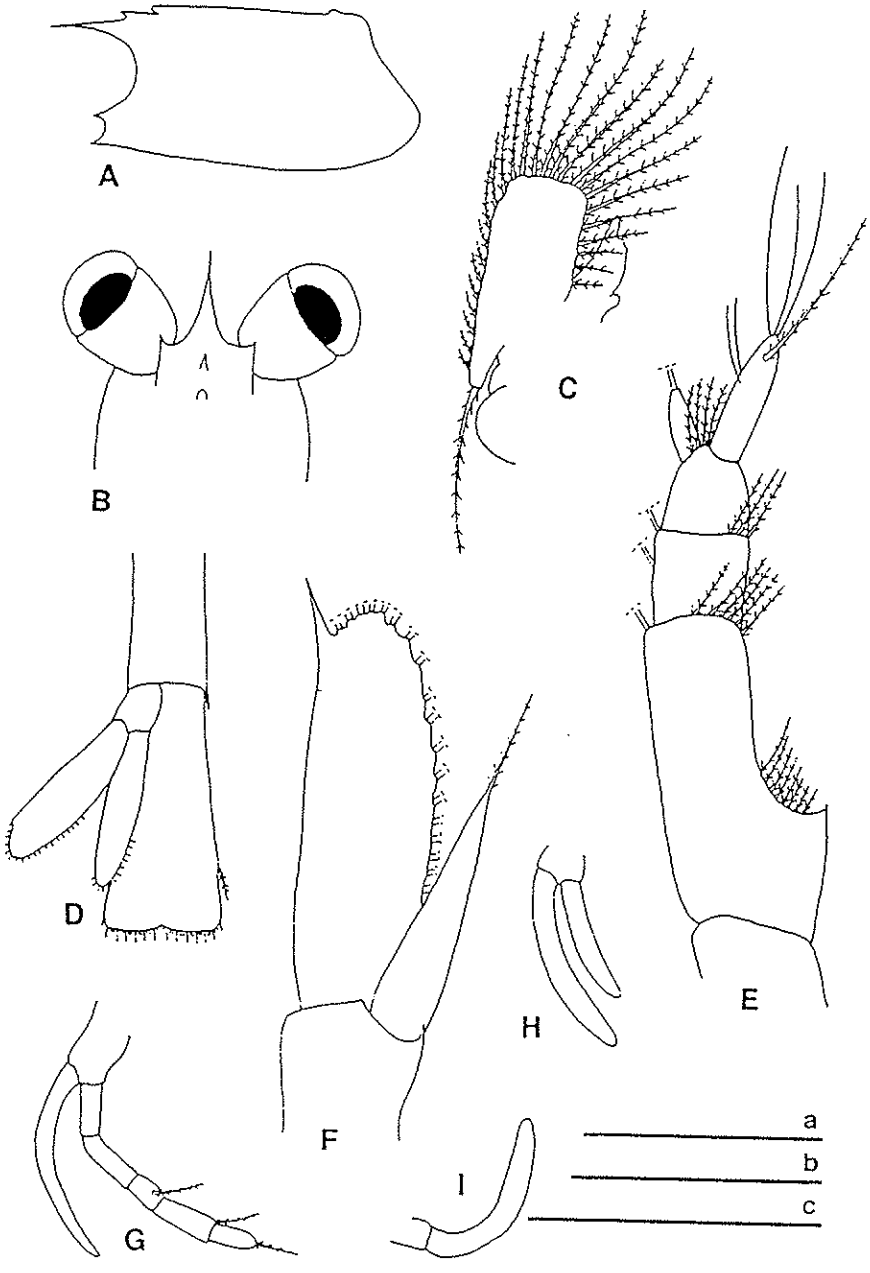

Figure 6. Zoea V. A: carapace. Lateral view; B: anterior part of carapace with cephalic appendages, dorsal view; C: scaphognathite of maxilla; D: uropods and telson; E: antennule; F: antenna; G: pereiopod III; H: pereiopod IV; I: pereiopod V. Scale bars: a = 1 mm (A–B, D); b = 0.5 mm (G–I); c = 0.5 mm (C, E–F).

Uropods (Fig. 6D).—Endouropod with 11 marginal setae; exouropod with 18 marginal setae; external terminal margin with 1 short spine.

Telson (Fig. 6D).—Posterior margin with 8+8 spines, external pair being located at distal quarter; telson longer, with nearly parallel lateral margins.

ZOEA VI

TL = 5.9 ± 0.28 mm; CL = 1.5 ± 0.15 mm; n = 8

General Characteristics (Fig. 7A,B).—Carapace with dorsal medial spine at rostral base; eyes pedunculate; carapace with one pair of dorsal spines on base of rostrum; rostrum generally more pronounced and straight; one pair of suborbital, antennal and pterygostomian spines.

Antennule (Fig. 7F).—Basal segment with eight distal external plumose setae and four marginal internal ones; stylocerite with seven plumose setae; medial segment with five distal external plumose setae and two marginal internal setae; distal segment with one marginal internal plumose seta and two large setae at base of medial lobe, the last bearing five setae; internal flagellum with one large plumodenticulate seta; external flagellum with 2, 3 and 3 proximal and distal aesthetascs, respectively, and one subterminal distal seta.

Antenna (Fig. 7E).—Exopodite with 20 long plumose setae; endopodite with two segments, basal one smaller, with one small subterminal spine.

Mandible.—Without palp; no other differences to previous stage.

Maxillule.—Coxal endite with 17 plumose setae; basal endite with 12 spines and three aesthetascs; no other differences to previous stage.

Maxilla (Fig. 7D).—Endopodite as in previous stage; proximal and distal lobe of coxal endite with 20+4 plumose setae, respectively; basal endite with nine plumodenticulate setae; scaphognathite with 36 marginal plumose setae.

Maxilliped I.—Basipodite with 4, 6, 7 and 6 plumodenticulate setae; no other differences to previous stage.

Maxilliped II.—Basipodite with 1, 2, 1, 3 and 3 plumose setae; exopodite with eight natatory plumose setae; no other differences from stages 4 and 5.

Maxilliped III.—Exopodite with 12 natatory plumose setae; carpus with one external and one internal seta; no other major differences.

Pereiopod I (Fig. 7G).—Basipodite with two simple setae; endopodite of five segments with 2, 1 and 1 setae on segments 1–3, respectively; propodus as long as dactylus, with one medial external plumose seta and two distal internal ones; dactylus with one strong terminal spine and two plumose setae.

Pereiopod II (Fig. 7H).—Basipodite with two simple setae; endopodite 5-segmented with 2, 1, and 1 setae on segments 1–3; propodus with two internal plumose setae; dactylus with one strong terminal spine and three plumose setae; exopodite with 16 natatory plumose setae.

Pereiopod III (Fig. 7I).—Basipodite as in pereiopod I and II; endopodite of five segments with 2, 1, 2, 6 and 1 setae; dactylus with one strong terminal spine and 1 small internal one; exopodite with 14 natatory plumose setae.

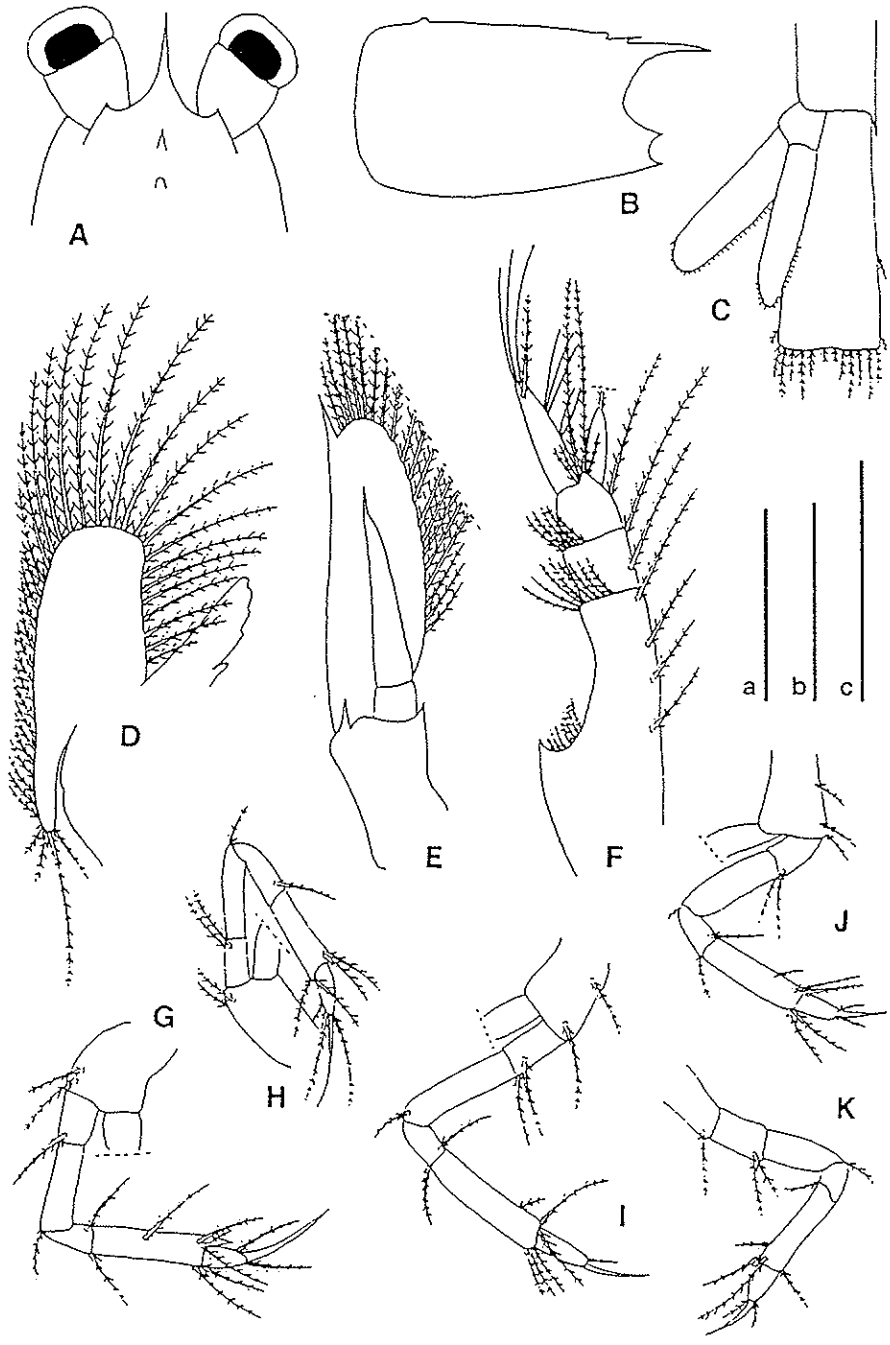

Figure 7. Zoea VI. A: anterior part of carapace with cephalic appendages, dorsal view; B: carapace, lateral view; C: uropods and telson; D: scaphognathite of maxilla; E: antenna; F: antennule; G: pereiopod I; H: pereiopod II; I: pereiopod III; J: pereiopod IV; K: pereiopod V. Scale bars: a = 1 mm (A–C); b = 0.5 mm (E–K); c = 0.5 mm (D).

Pereiopod IV (Fig. 7J).—Basipodite with three setae; endopodite of five segments with 2, 1, 2, 5 and 2 distal and proximal setae, respectively; dactylus with one strong terminal spine; exopodite with 12 pairs of plumose setae.

Pereiopod V (Fig. 7K).—Uniramous; endopodite of five segments with 2, 1, 1, 4 and 2 proximal and distal setae, respectively; dactylus with one strong terminal spine; basipodite with one plumose seta.

Pleopods.—Rudimentary buds in segments 2–5.

Uropods (Fig. 7C).—Endouropod with 21 marginal setae; exouropod with well developed external spine and 25 marginal setae; no other differences to previous stage.

Telson (Fig. 7C).—Lateral margins almost parallel; posterior margin with 8+8 processes, lateral pair located at distal third.

Discussion

The main two issues addressed by the morphological comparisons in the herein presented work are (1) differences between two populations from Chilean Pacific coastal waters and the southwestern Atlantic (see methods), being geographically separated by the Chilean South Patagonian Icefield (SPI), and (2) differences between laboratory-reared and field-collected larvae.

(1) *N. magellanica* is one of the most widely distributed hippolytid shrimps of South America with a geographical range of approximately 35° of latitude (Wehrtmann and Kattner, 1998), and the only of its genus which is known to occur in Chilean as well as in Argentine waters (Retamal, 1981; Boschi et al., 1981, 1992; Arntz et al., 1996; Spivak, 1997; Wehrtmann and Albornoz, 1998). Larvae of the two populations compared in this study are geographically separated by the Chilean South Patagonian Icefield (Campos de Hielo Sur; Warren and Sugden, 1993) which extends about 460 km along the Chilean Pacific coast, and where *N. magellanica* was shown to be absent. In fact, only eight decapod species have been recorded in the SPI yet, contributing less than 5% of the Chilean decapod fauna in general (Mutschke et al., 1996; see also Retamal, 1981). This faunal impoverishment in decapods was discussed to be due to lower average temperatures, salinity as well as sediment input and ice impact due to glaciers (cf U.S. Navy, 1982; Peters and Breeman, 1993; Sievers et al., 1996). *N. magellanica* is one of the most abundant shrimps on the continental slope of southern South America. An aggregation of older larval stages in potential coastal recruitment habitats was observed during our investigations, whereas early zoeae were found widely distributed in the open sea (Fig. 1).

Hippolytid larvae obtained during our investigation were clearly identified as belonging to *N. magellanica*. Apart from some differences (Table 1), the general scheme and morphological features correspond the larval description of Wehrtmann and Albornoz (1998). Only two other hippolytid species (*Chorismus tuberculatus*, *Chorismus antarcticus*) are known to occur in our sampling area in the southwestern Atlantic, and they can easily be distinguished from the studied species (see Gurney, 1937; Thatje and Bacardit, 2000). Distinctive characters distinguishing *N. magellanica* from the latter two hippolytid species are:

- Zoea I with small rostral spine.
- Margins of carapace smooth, reduced supraorbital spines and pterigostomian spines present.

Table 1. Differences in morphological characters (average observations) of *Nauticaris magellanica* between a population off central Chile (according to Wehrtmann and Albornoz, 1998) and the present investigation performed in the southwestern Atlantic Ocean. Pacific population (Chile) = Pacific. Southwestern Atlantic population (Argentina) = Atlantic. No difference = (-).

	Zoea I		Zoea II		Zoea III	
Character	Pacific	Atlantic	Pacific	Atlantic	Pacific	Atlantic
Mean TL	1.40 mm	2.2 mm	1.85 mm	2.9 mm	2.25 mm	3.9 mm
Mean CL	0.30 mm	0.6 mm	0.04 mm	0.7 mm	0.47 mm	1.0 mm
Rostrum	-	-	-	-	-	-
Antennule	-	-	External Flagellum with 3 aesthetascs + 1 seta	External Flagellum with 4 aesthetascs + 1 seta	-	-
Antenna	Exopodite with 7+2 setae	Exopodite with 9+2 setae	-	-	-	-
Maxillule	Endopodite with 3+2 setae	Endopodite with 3+12 setae	Coxal endite with 7+4 setae	Coxal endite with 11+4 setae	-	-
Maxilla	-	-	-	-	Coxal endite with 8+4 setae	Coxal endite with 13+4 setae
Maxilliped I	Endopodite with 3,1,3,1 setae	Endopodite with 3,1,2,4 setae	-	-	-	-

Table 1. Continued.

Character	Zoea I		Zoea II		Zoea III	
	Pacific	Atlantic	Pacific	Atlantic	Pacific	Atlantic
Maxilliped II	Basipodite with 1,2,3,3 setae; expodite with 5+2 setae	Basipodite with 2,3,3,0 setae; expodite with 3+2 setae	-	-	-	-
Maxilliped III	-	-	-	-	Expodite with 7 setae	Expodite with 8 setae
Pereiopod I	rudimentarious buds	absent	-	-	Endopodite with 1,0,0,2,4 setae	Endopodite with 2,1,0,2,3 setae
Pereiopod II	rudimentarious buds	absent	-	-	-	-
Pereiopod III	-	-	absent	rudimentarious bud	-	-
Pereiopod IV	-	-	-	-	absent	uniramous simple buds
Pereiopod V	-	-	-	-	absent	uniramous simple buds
Pleopods	-	-	-	-	-	-
Uropods	-	-	developing buds visible	-	-	-
Telson	-	-	-	-	-	-

Table 1. Continued.

Character	Zoea IV		Zoea V		Zoea VI	
	Pacific	Atlantic	Pacific	Atlantic	Pacific	Atlantic
Mean TL	2.64 mm	4.03 mm	2.88 mm	4.68 mm	3.17 mm	5.9 mm
Mean CL	0.56 mm	1.03 mm	0.61 mm	1.1 mm	0.64 mm	1.5 mm
Rostrum	-	-	with 2 simple setae	no setae	with 2 simple setae	no setae
Antennule	External Flagellum with 4 aesthetascs + 2 seta	External Flagellum with 3 aesthetascs + 1 seta	-	-	External Flagellum with 4 aesthetascs + 2 seta	External Flagellum with 8 aesthetascs + 1 seta
Antenna	-	-	-	-	-	-
Maxillule	-	-	-	-	-	-
Maxilla	-	-	-	-	Scaphognathite with 18–25 setae	Scaphognathite with 36 setae
Maxilliped I	-	-	Coxopodite with 10 setae; basipodite with 4,5,6,4 setae	Coxopodite with 8 setae; basipodite with 4,5,5,6 setae	Basipodite with 4,6,6,6 setae	Basipodite with 4,6,7,6 setae
Maxilliped II	-	-	-	-	Basipodite with 1,1,1,1,0 setae	Basipodite with 1,2,1,3,3 setae

Table 1. Continued.

Character	Zoea IV		Zoea V		Zoea VI	
	Pacific	Atlantic	Pacific	Atlantic	Pacific	Atlantic
Maxilliped III	-	-	-	-	-	-
Pereiopod I	Caxopodite without setae; endopodite with 0,0,0,0,5 setae	Caxopodite with 2 setae; endopodite with 1,0,0,1,2 setae	-	-	-	-
Pereiopod II	-	-	-	-	Exopodite with 13 setae	Exopodite with 14 setae
Pereiopod III	-	-	Endopodite with 8–9 setae	Endopodite without setae	Endopodite with 11–12 setae	Endopodite with 14 setae
Pereiopod IV	-	-	-	-	Exopodite with 8–9 setae	Exopodite with 12 setae
Pereiopod V	absent	simple buds	-	-	-	-
Pleopods	-	-	-	-	absent	Buds in segments 2–5
Uropods	-	-	-	-	Endouropod with 11–18 setae; exouropod with 16–22 setae	Endouropod with 21 setae; exouropod with 25 setae
Telson	-	-	-	-	-	-

- Maxillule with external seta.
- Exopodites present on pereiopods 1-4.
- Somites 4 and 5 without lateral spines.
- No anal spine.
- Posterior margin of telson straight in all stages, with 7+7 posterior processes, lateral pair located at distal third.

Due to the absence of complete larval descriptions of species other than *N. magellanica*, it is not possible to point out general characters which separate this genus from other genera of the Hippolytidae. At least for the southwestern Atlantic, the above mentioned characteristics allow a clear separation from the other hippolytid shrimps.

In the case of *N. magellanica*, morphological variability can be discussed as an ecological strategy and adaptation to changing environmental conditions. Most obvious differences in larval morphology of *N. magellanica* occurred in total larval length, being over 1.5 times bigger in the southwestern Atlantic as compared to the material studied by Wehrtmann and Albornoz (1998) from northern Chile (Table 1). Wehrtmann and Kattner (1998) observed a latitudinal increase in egg-size of *N. magellanica* at the Chilean Pacific coast which, in addition to the increase in larval size, confirms part of the reproductive theories for marine benthic invertebrates postulated by Thorson (1936, 1950), later known as "Thorson's rule" which was originally related to latitudinal changes in temperature. However, this rule has been discussed controversially during the last decade (Pearse et al., 1991; Hoegh-Guldberg and Pearse, 1995), but was often testified to be valid at least in gastropods and decapods (e.g., Thorson, 1950; Gorny et al., 1993; Clarke, 1993; Thatje et al., in review). Waters of northern Chile show higher, and greater fluctuating temperatures (winter/summer 14–24°C) than the southwestern Atlantic (winter/summer 4–10°C) (e.g., Medeiros and Kjerfve, 1988; Peters and Breeman, 1993), thus may explain the necessity of energy saving strategies by developing big-sized eggs and first zoeae, and a shorten planktonic larval development in the Atlantic population of *N. magellanica*. The early determination of the pereiopods III to V from Zoea II to IV, respectively (Table 1), supports this view towards a more abbreviated larval development in the southwestern Atlantic in contrast to northern Chile (Clarke, 1987, 1993).

Apart from larval size, main features characterizing larvae of *N. magellanica*, such as the rostrum, telson and uropods, did not show strong variability (Table 1), and therefore larvae of both compared populations may in some cases show identical morphology. However, we are not sufficiently able to explain the great observed variability in the number of setae, especially on thoracopods (Table 1), between both compared populations, just using terms of functional morphology or ecological adaptation. Future investigations need to confirm, if such variability is a common pattern in the larval development of other species, too, or if these basic morphological differences are a hint at a species split-off of two geographically separated populations of *N. magellanica* (for discussion see also Thatje and Bacardit, 2000).

(2) Rearing larvae under laboratory conditions was often proposed to be the best method for analyzing developmental pathways in marine invertebrates, mainly, because it allows a clear relation of larvae to the species. Variability in both larval morphology and the number of larval instars before metamorphosis has been described since first complete laboratory culturing of decapod development succeeded (Boyd and Johnson, 1963; Campodonico and Guzmán, 1981; Gore and Scotto, 1982), and was shown to be especially conspicuous in a variety of caridean shrimps (e.g., Knowlton, 1974; Christiansen

and Anger, 1990; Wehrtmann, 1991). Published comparisons between laboratory-reared and field-collected larvae do not exist, although larval variability is generally assumed to occur in nature, too, and to be an important factor in the development of carideans, enhancing survival and dispersal of larvae (e.g., Fincham and Figueras, 1986; Villamar and Brusca, 1988; Wehrtmann, 1991).

Wehrtmann and Albornoz (1998) described nine zoeal stages with the number of instars extending up to eleven in laboratory-reared larvae of *N. magellanica,* whereas our field-collected larvae divided into only six clear zoeal stages. It was frequently shown that caridean morphogenesis is affected by distinctive biotic and abiotic factors such as temperature, salinity and food availability (e.g., Villamar and Brusca, 1988; Christiansen and Anger, 1990). These factors are hardly possible to control in rearing experiments, because in most cases species ecology is rather unknown and mass-culturing is proposed to provide finally at least some juveniles. This may also be one reason why mortality rates in larvae cultures are in most cases dramatically high. However, if we assume that great variability in larval instars in laboratory cultures appears to be a reaction to physical and chemical stress, biased by unstable rearing conditions, and resulting in different developmental pathways in one culture (compare with Wehrtmann and Albornoz, 1998), why does larval development seem to be less variable in nature?

One possibility explaining these circumstances might be that the ability of meroplanktonic larvae, especially early developmental stages, to move actively is rather limited. Larvae are tied to water masses they are released to, and therefore distribution over greater distances is realized by transport by means of currents (for discussion see Banse, 1955; Dooley, 1977; Thatje et al., 1999), and for this reason environmental conditions can be more stable than in artificial rearing experiments. Developmental pathways may not necessarily depend on flexibility in larval instars, but in the case of changes in environmental conditions, such as mixture of water masses, food deficiency or changes in temperature and salinity, this flexibility is an evolutional and ecological strategy which enhances survival and allows distribution of larvae over greater distances.

Acknowledgments

The first author acknowledges the intensive support of his work in South America by the International Bureau of the German Ministry of Research (BMBF) and the Alfred Wegener Institute for Polar and Marine Research, Germany. Our thanks are also due to three anonymous reviewers for their helpful comments on an earlier draft which improved this work considerably. This is Alfred Wegener Institute publication No. 1670.

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DATE SUBMITTED: June 22, 1999. DATE ACCEPTED: December 30, 1999.

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JOURNAL OF CRUSTACEAN BIOLOGY, 21(2): 492–505, 2001

DESCRIPTION AND KEY TO THE ZOEAL STAGES OF THE CAMPYLONOTIDAE (DECAPODA, CARIDEA) FROM THE MAGELLAN REGION

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ABSTRACT

The present work provides a first description of the zoeal stages of the Caridean prawns *Campylonotus vagans, C. semistriatus* and *C. capensis* Bate, 1888. Zoeal stages one and two were obtained from plankton catches during several expeditions in the Magellan region and the southwestern Atlantic Ocean, and first zoeae of *C. vagans* were confirmed with larvae hatched in a laboratory culture. Based on the results obtained, we conclude the morphological differences of the presence/absence of carapace spines, the shape of the somites, the telson and its number of posterolateral spines to serve as diagnostic features for the determination of campylonotid larvae. Morphological comparisons with larvae of the Pandalidae, Palaemonidae, and Oplophoridae suggest the Campylonotidae to be phylogenetically related to the Oplophoridae. Additionally, a key for identifying the zoeal stages of the Campylonotidae from the southernmost region of America is given in order to facilitate future ecological and life history studies.

RESUMEN

El presente trabajo provee una primera descripción para los estadíos larvales de los camarones Caridea *Campylonotus vagans, C. semistriatus* y *C. capensis* Bate 1888. Los estadíos larvales de las zoeas uno y dos fueron obtenidos con una red de plancton durante varias expediciones en la Región Magallánica y en el Océano Atlántico sudoccidental y el estadío uno de *C. vagans* fue también confirmado con larvas eclosionadas de huevos en el laboratorio. Basándonos en los resultados obtenidos, concluimos que las diferencias morfológicas de presencia/ ausencia de espinas en el cefalotórax, el aspecto de los somites, del telson y su número de espinas postlaterales sirven como caracteres diagnóstico para la determinación de las larvas de Campylonotidae. Las comparaciones morfológicas de las larvas de Campylonotus con las de las familias Pandalidae, Palaemonidae, y Oplophoridae reflejan mayor afinidad filogenética con las de esta última familia. Se presenta una clave para identificar los estadíos larvales de los Campylonotidae en aguas de América del Sur y para facilitar estudios ecológicos y de ciclos de vida.

The knowledge of benthic invertebrates and their larvae from the subantarctic Magellan region is currently very limited (e.g., Thatje and Mutschke, 1999; Lovrich, 1999). There is still a lack of ecological studies on, and especially descriptions and keys for the identification of, meroplanktonic larvae. Only decapod larvae have been investigated more closely; thus, larval descriptions are available for the most common species occurring in the Magellan region (Albornoz and Wehrtmann, 1997; Wehrtmann and Báez, 1997; Lovrich, 1999). Even now, only the first zoeal stage of *Campylonotus rathbunae* Schmitt, obtained from laboratory culturing, has been described by Pike and Williamson (1966). Although this species is not present in the southwestern Atlantic and the Magellan region, very similar larvae were found in plankton samples obtained during various expeditions from 1978 to 1998 which were identified as belonging to *Campylonotus*.

The Caridean prawn *Campylonotus vagans* occurs in wide parts of the Chilean coast south to the Magellan region, as well as in the southwestern Atlantic Ocean of Argentina. *Campylonotus semistriatus* is restricted to the channels and fjords of the Magellan region

and the southwestern Atlantic, and a third species, *C. capensis,* is known to be distributed only in the southwestern Atlantic (Fig. 1; Torti and Boschi, 1973; Retamal, 1981; Spivak, 1997; Gorny, 1999). The present work provides new descriptions of the campylonotid larval stages in order to facilitate future studies on larval ecology, life history, and stock recruitment.

Additionally, we present a key to the larvae of all three species from the Magellan region, which allows the determination of planktonic campylonotid larvae from the Chilean and Argentine coasts. Furthermore, we compare these descriptions with those of Pike and Williamson (1966) for *C. rathbunae.*

Materials and Methods

The material studied was collected in 1978 by the German vessel "Walther Herwig" during cruises III/1 (5th leg) and III/2 (6th leg) carried out on the Argentine shelf and continental slope in the southwestern Atlantic Ocean (Fig. 1). Samples were collected vertically from the seafloor to the surface or 100 m to the surface by means of a Bongo net of 330 µm mesh size and were preserved in 3% Formalin solution buffered with hexamethylenetetramine. Complete descriptions of the cruises and additional information on oceanographic measurements can be obtained from Ciechomski *et al.* (1979) and Cousseau *et al.* (1979).

The larval material caught during the "Walther Herwig" cruises has been compared to the material collected by a plankton net of 200 µm mesh size by monthly sampling from onboard a Zodiac in the Beagle Channel (Tierra del Fuego) from 1987 to 1989 (see Lovrich, 1999).

The first zoeal stage of *C. vagans* was confirmed with larvae hatched in laboratory culturing of ovigerous females with an advanced embryonic egg stage, which were collected with an epibenthic trawl from onboard an inflatable dinghy in the Beagle Channel (Magellan region, Fig. 1) in September 1999.

Carapace (CL) and total (TL) lengths of the larvae were measured from the base of the rostrum between the eyes to the posterior dorsal margin of the carapace and to the posterior margin of the telson, respectively. The terminology used for the differentiation of the larval phases, the larval morphology and the characteristics between species and larval stages, corresponds to that suggested by Williamson (1960, 1968, 1982), Gurney (1942), Boschi (1981), Haynes (1978, 1981, 1985), and Clark *et al.* (1998).

Results

Family Campylonotidae

Campylonotus vagans Bate, 1888

Zoea I.—(Fig. 2): TL = 5.8 ± 0.06 mm; CL = 1.9 ± 0.01 mm; n = 18.

Cephalothorax (Fig. 2A). Rostrum straight, without dorsal spines at base. Eyes sessile.

Antennule (Fig. 2E). Uniramous. Peduncle unsegmented, with 1 long plumose seta at inner distal end. Endopod absent. Exopod unsegmented, with 4 aesthetascs and 1 subterminal plumose seta.

Antenna (Fig. 2D). Biramous. Protopod unsegmented, with 1 well-developed spine at inner distal end and 1 shorter terminal central spine. Endopod unsegmented, with 1 long apical plumose seta. Exopod (scaphocerite) with 10 terminal plumose setae and 1 long plumose medial seta.

Mandible (Fig. 2F). Well-developed molar and incisor processes, with lacinia mobilis. Palp absent.

Maxillule (Fig. 2G). Coxal endite with 20 plumodenticulate setae. Basial endite with 13 or 14 plumodenticulate setae. Endopod 2-segmented, proximal segment with 2 plumodenticulate setae, distal segment with 3 terminal plumodenticulate setae. Two simple setae at base of endopod. Exopod absent.

Maxilla (Fig. 2H). Coxal endites proximally and distally with 26 and 4 setae, respectively. Basal endites with 12 setae at each side. Endopod 2-segmented, proximal segment with 3, 2 setae and distal segment with 5 setae arranged 1, 2, 2. Exopod (scaphognathite) with 30–32 marginal plumose setae.

Maxilliped 1 (Fig. 2I). Coxa and basis with 8 and 29–31 setae, respectively. Endopod 4-segmented with 9 plumodenticulate setae arranged 2+0, 2+0, 2+0, 3 terminal. Exopod unsegmented, with 9 long terminal plumose natatory setae. Epipod present.

Maxilliped 2 (Fig. 2J). Coxa with 2 medial plumodenticulate setae. Basis with 9 medial plumodenticulate setae arranged 3, 3, 3. Endopod 5-segmented, with 14 plumodenticulate setae arranged 2+1, 2+1, 0+1, 2+1, 4 terminal. Exopod unsegmented, with 14 long terminal plumose natatory setae. Epipod present.

Maxilliped 3 (Fig. 2K). Coxa unarmed. Basis with 4 medial plumodenticulate setae arranged 2, 2. Endopod 5-segmented, with 13 plumodenticulate setae arranged 3+0, 1+1, 1+0, 2+1, 4 terminal. Exopod unsegmented, with 17 long terminal plumose natatory setae. Epipod present.

Pereiopods (Fig. 2L–P). Pereiopod 1, endopod 5-segmented; segments 1–3 without setation; propodus with 2 plumose distal setae; dactylus with 2 apical setae; exopod unsegmented, without setation. Pereiopod 2, endopod 5-segmented, segments 1–3 without setation; propodus with 1+1 plumose setae, dactylus with 1 terminal plumose seta; exopod unsegmented, without setation. Pereio-

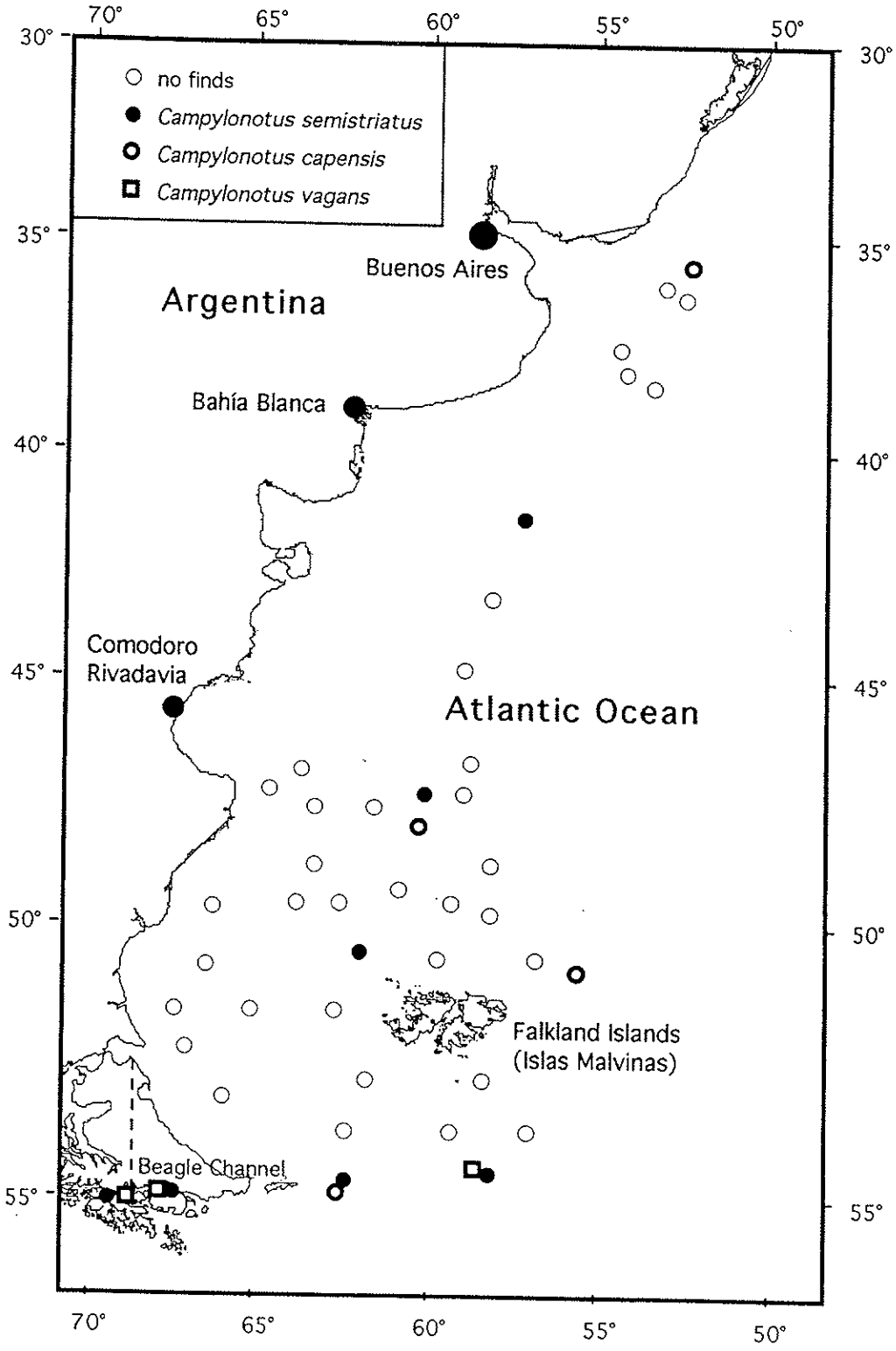

Fig. 1. Sampling locations of campylonotid larvae in the Magellan region and the southwestern Atlantic Ocean.

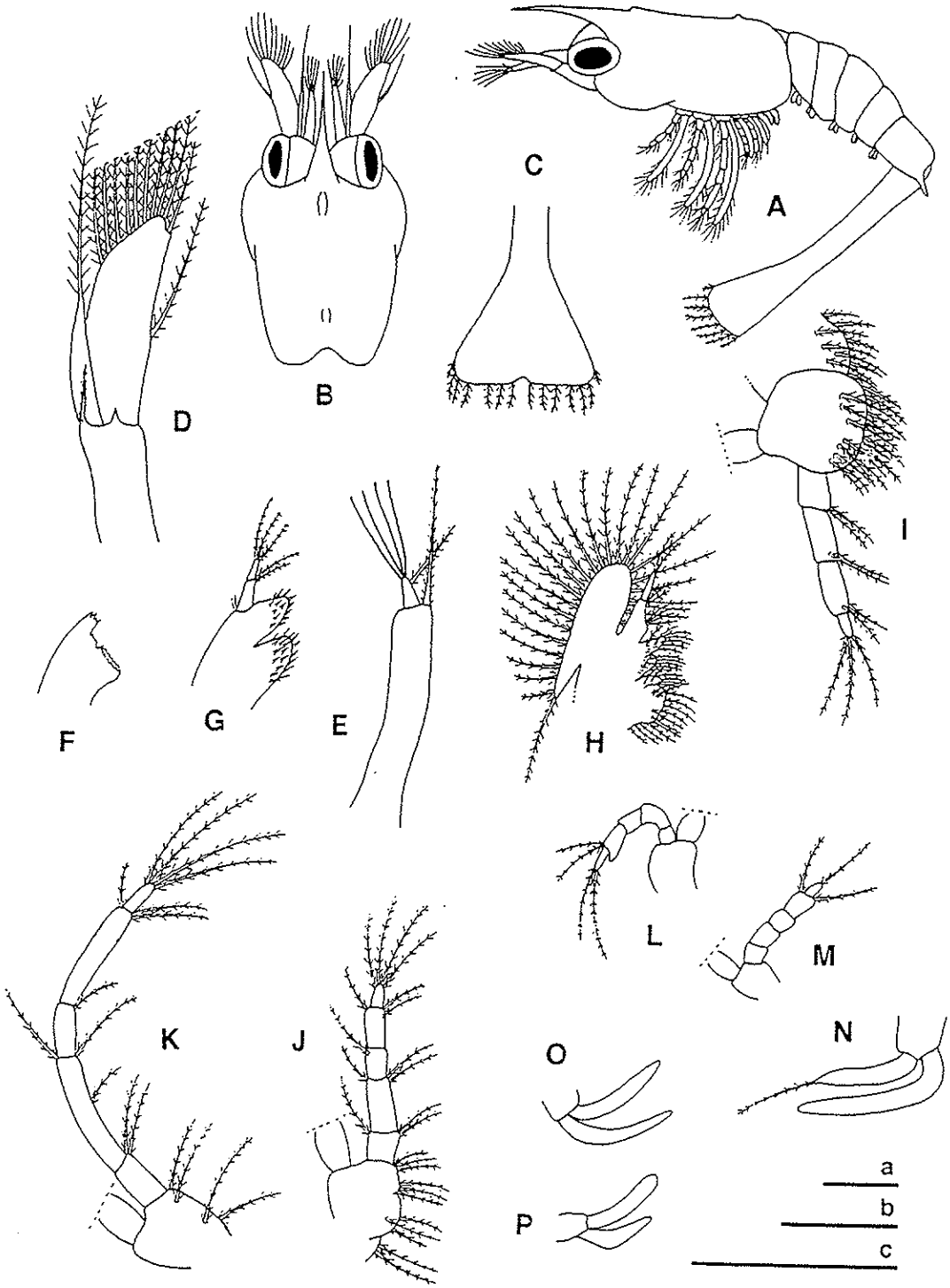

Fig. 2. First zoeal stage of *Campylonotus vagans;* A, whole animal, lateral view; B, carapace with cephalic appendages, dorsal view; C, telson, ventral view; D, antenna; E, antennule; F, mandible; G, maxillule; H, maxilla; I, maxilliped 1, lateral view; J, maxilliped 2, lateral view; K, maxilliped 3, lateral view; L, pereiopod 1, lateral view; M, pereiopod 2, lateral view; N, pereiopod 3, lateral view; O, pereiopod 4, lateral view; P, pereiopod 5, lateral view. Scale bars: a = 1 mm (Figs. A–C); b = 0.5 mm (Figs. D–K); c = 1 mm (Figs. L–P).

pod 3, endopod unsegmented, with 1 terminal plumodenticulate seta; exopod slightly longer than endopod, unsegmented, unarmed. Pereiopods 4 and 5, rudimentary, biramous.

Abdomen (Fig. 2A). Five abdominal somites, without expansions or ornamentation. Somite 5 with 1 long spine on posterolateral margin. Pleopods absent.

Telson (Fig. 2C). Triangular, with strong medial cleft and 7 pairs of processes on posterior margin.

Zoea II.—(Fig. 3): TL = 6.9 ± 0.05 mm; LC = 2.0 ± 0.03 mm; n = 9.

Cephalothorax (Fig. 3A). Rostrum straight, smooth, with 2 dorsal spines at base. Pterygostomic and supraorbital spines present, the last well developed. One dorsal posterior protuberance. Eyes now stalked.

Antennule (Fig. 3C). Peduncule 3-segmented, first segment with one conspicuous medial spine, 2+6 terminal plumodenticulate setae, stylocerite rudimentary, reduced to small bud near base; second and third segments with 2+4 and 1+5+1+5 plumodenticulate setae, respectively. Endopod now present, with small, apical simple seta. Exopod unsegmented, with 13 aesthetascs, arranged 3, 3, 3, 4.

Antenna (Fig. 3D). Endopod 3-segmented, basial segment unarmed, second segment with 1 plumodenticulate seta, distal segment with 1 apical simple seta. Exopod (scaphocerite) with 27–29 plumodenticulate setae. No other changes.

Mandible (Fig. 3B). Unchanged.

Maxillule (Fig. 3E). Basial endite with 25 plumodenticulate setae. No other changes.

Maxilla (Fig. 3I). Basial endite with 13+14 plumodenticulate setae. Endopod unsegmented, with 10 plumodenticulate setae, arranged 3, 2, 1, 2, 2. Scaphognathite now with 30 or 31 plumose marginal setae. No other changes.

Maxilliped 1 (Fig. 3F). Basis with 34 plumodenticulate setae. Exopod with 12 long terminal plumose setae. No other changes.

Maxilliped 2 (Fig. 3G). Exopod now with 18 long terminal plumose natatory setae. No other changes.

Maxilliped 3 (Fig. 3J). Basis with 5 medial plumodenticulate setae. Endopod 5-segmented, with 17 plumodenticulate setae, arranged 3+0, 2+2, 0+2, 4+2, 2 terminal. No other changes.

Pereiopods (Fig. 3K–O). Pereiopod 1, basis with 4 plumodenticulate setae, endopod 5-segmented, ischium, merus, carpus, propodus, and dactylus with 2, 2, 3, 7, 3 plumodenticulate setae, respectively; propodus and dactylus as well-developed chela; exopod with 16 plumose setae. Pereiopod 2, basis with 3 plumodenticulate setae, endopod 5-segmented, ischium, merus, carpus, propodus, and dactylus with 2, 2, 2, 7, 3 plumodenticulate setae, respectively (dactylus with 1 strong apical spine), propodus and dactylus as well-developed chela; exopod with 16 plumose setae. Pereiopod 3, basis with 4 plumodenticulate setae, endopod 5-segmented, with 2, 3, 2, 4, 3 plumodenticulate setae, respectively; exopod with 16 plumose setae. Pereiopod 4, basis with 2 plumodenticulate setae, endopod 5-segmented, with 2, 3, 3, 5, 2 plumodenticulate setae (dactylus with 1 apical spine), exopod with 12 plumose setae. Pereiopod 5, endopod 5-segmented, with 0, 3, 2, 5, 2 plumodenticulate setae, respectively (dactylus with 1 apical spine), exopod reduced and unarmed.

Abdomen (Fig. 3A). Spine on posterolateral margin of somite 5 relatively shorter. Pleopodal buds present. No other changes.

Telson (Fig. 3H). One new pair of processes (now 8 pairs) at inner posterior margin. Uropods biramous, unarmed.

Campylonotus semistriatus Bate, 1888

Zoea I.—(Fig. 4): TL = 8.4 ± 0.08 mm; CL = 2.2 ± 0.02 mm; n = 13.

Cephalothorax (Fig. 4A). Rostrum straight, with 15 small spines; anteroventral margin with pterygostomic spine and 14 denticles. Two dorsal protuberances. Eyes sessile.

Antennule (Fig. 4D). Uniramous. Peduncle unsegmented, with inner distal plumose seta. Endopod absent. Exopod unsegmented, with 4 aesthetascs and one subterminal plumose seta.

Antenna (Fig. 4E). Biramous. Protopod unsegmented, no terminal spine, 1 medial and 1 terminal spine on outer margin. Endopod unsegmented, with 1 long apical plumose seta and well-developed inner spine; spinulose ventral spine at base of endopod. Exopod (scaphocerite) with 11 terminal plumose setae and 1 long plumose medial seta.

Mandible (Fig. 4F). Well-developed molar and incisor processes; with lacinia mobilis. Palp absent.

Maxillule (Fig. 4G). Coxal endite with 20–22 plumodenticulate setae. Basial endite

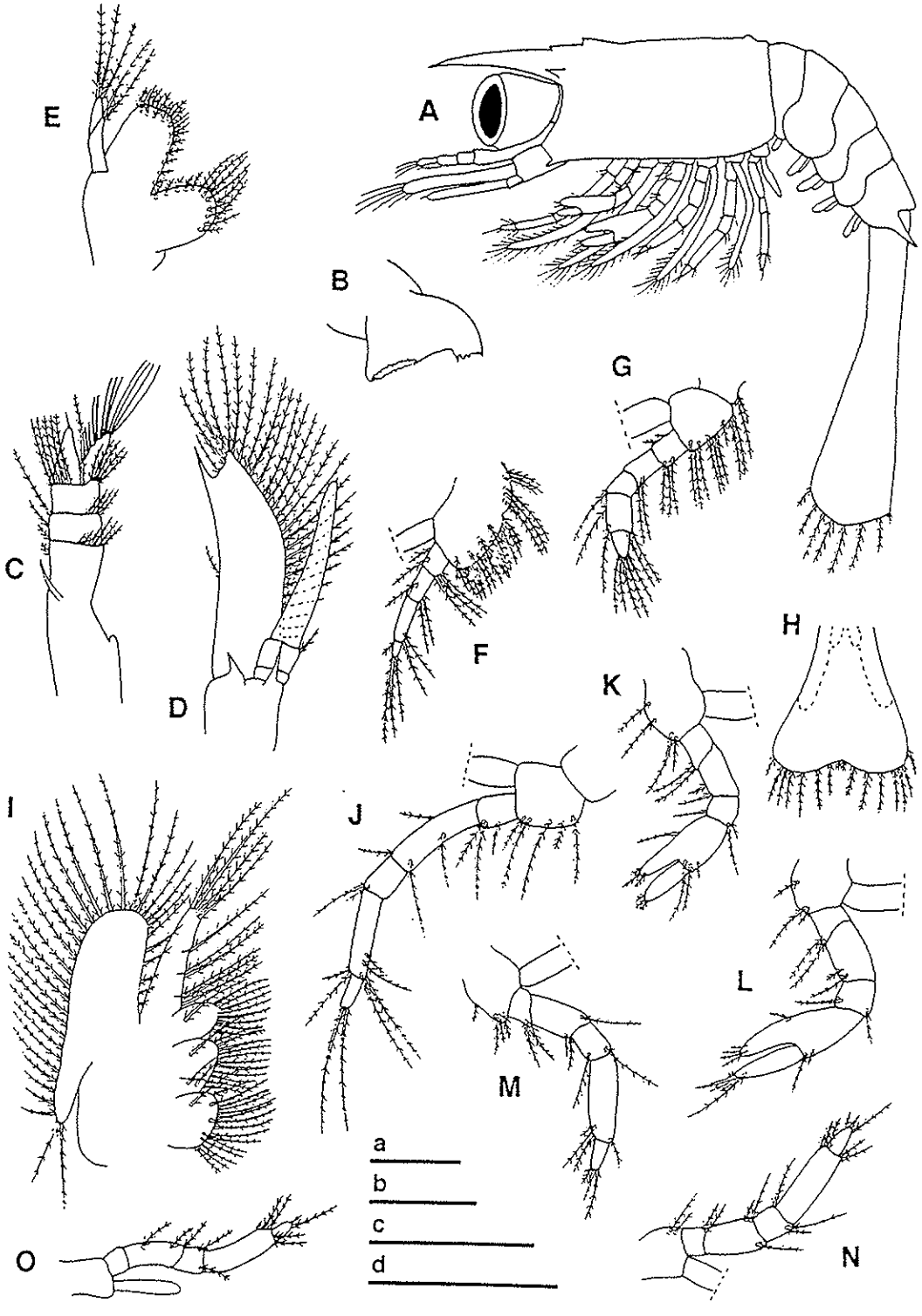

Fig. 3. Second zoeal stage of *Campylonotus vagans;* A, whole animal, lateral view; B, mandible; C, antennule; D, antenna; E, maxillule, aboral view; F, maxilliped 1, lateral view; G, maxilliped 2, lateral view; H, telson, ventral view; I, maxilla; J, maxilliped 3, lateral view; K, pereiopod 1, lateral view; L, pereiopod 2, lateral view; M, pereiopod 3, lateral view; N, pereiopod 4, lateral view; O, pereiopod 5, lateral view. Scale bars: a = 1 mm (Fig. H); b = 1 mm (Fig. A); c = 0.5 mm (Figs. B, E, I); d = 1 mm (Figs. C, D, F, G, J–O).

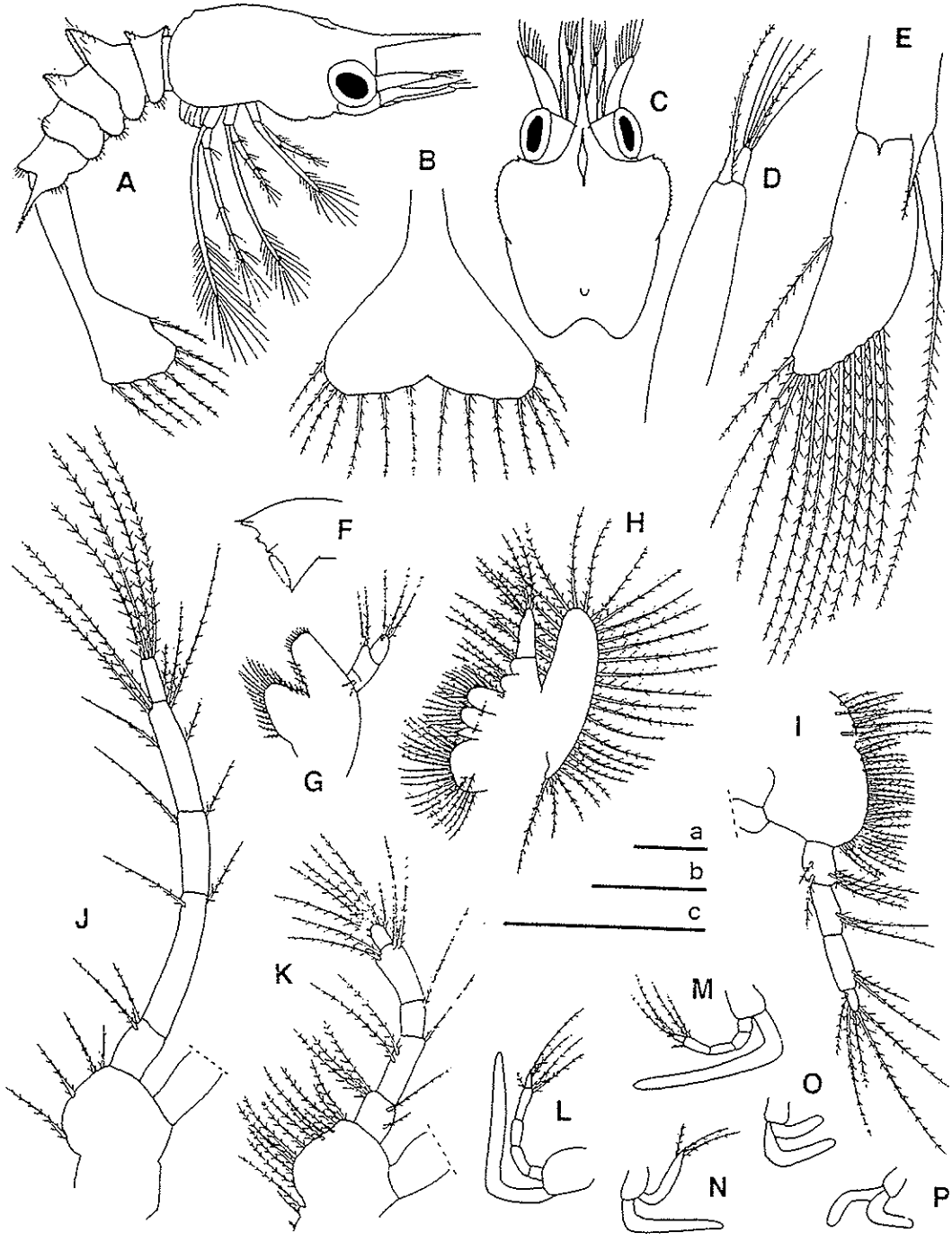

Fig. 4. First zoeal stage of *Campylonotus semistriatus*: A, whole animal, lateral view; B, telson, ventral view; C, carapace, dorsal view; D, antennule; E, antenna; F, mandible; G, maxillule, aboral view; H, maxilla, aboral view; I, maxilliped 1, lateral view; J, maxilliped 3, lateral view; K, maxilliped 2, lateral view; L, pereiopod 1, lateral view; M, pereiopod 2, lateral view; N, pereiopod 3, lateral view; O, pereiopod 4, lateral view; P, pereiopod 5, lateral view. Scale bars: a = 1 mm (Figs. A–C); b = 0.5 mm (Figs. D–K); c = 1 mm (Figs. L–P).

with 13 or 14 spines and 4 setae. Endopod 2-segmented, with 2+3 setae, respectively. Two short, simple setae at base of endopod. Exopod absent.

Maxilla (Fig. 4H). Proximal endite of coxa with about 26 setae, distal endite small, bearing 4 setae. Basal endites with 12 setae each. Palp with indications of 5 segments, partial division between first and second, complete division between second and third, segments with 3, 2, 1, 2, 2 setae from proximal to distal, respectively. Exopod (scaphognathite) with 30–32 plumose marginal setae and 1 terminal flagellum with setules.

Maxilliped 1 (Fig. 4I). Coxa and basis with 11 and 29–31 medial plumodenticulate setae respectively. Endopod 4-segmented, with 14 plumodenticulate setae, arranged 3+2, 2+0, 2+0, 4+1 (1 subterminal, 4 terminal) setae, respectively. Exopod unsegmented, with 14 long plumose natatory setae. Epipod present.

Maxilliped 2 (Fig. 4K). Coxa with 2 medial plumodenticulate setae. Basis with 12 medial plumodenticulate setae, arranged 4, 4, 4. Endopod 5-segmented, with 3+2, 2+1, 0+1, 2+2, 5+1 (1 subterminal, 5 terminal) setae, respectively. Exopod unsegmented, with 16 long plumose natatory setae. Epipod present.

Maxilliped 3 (Fig. 4J). Coxa unarmed. Basis with 4 medial plumodenticulate setae, arranged 1, 1, 2. Endopod 5-segmented with 2+0, 1+1, 1+1, 3+3, 4+1 (1 subterminal, 4 terminal) setae, respectively. Exopod unsegmented with 26 long terminal plumose natatory setae. Epipod present.

Pereiopods (Fig. 4L–P). Pereiopods 1 and 2, endopod 5-segmented, with 0, 0, 0, 2+1, 2 setae, respectively; with indications of chelae; exopod slightly longer than endopod. Pereiopod 3, endopod unsegmented, with 2 terminal and 1 subterminal setae; exopod slightly longer than endopod. Pereiopods 4 and 5 rudimentary, biramous.

Abdomen (Fig. 4A). First somite with expanded anterior and posterior dorsal margins; somites 2–5 with only posterior dorsal margins expanded. Somite 5 with 1 long spine on posterolateral margin. Ventral and posterior dorsal margins of all somites fringed with large denticles; fine large plumose setae on dorsal and ventral surface. Somite 6 continuous with telson. Pleopods absent.

Telson (Fig. 4B). Triangular, with strong medial cleft and 7 pairs of processes on posterior margin.

Zoea II.—(Fig. 5): TL = 12 ± 0.01 mm; CL = 3.4 ± 0.03 mm; n = 11.

Cephalothorax (Fig. 5A). Rostrum with 9 dorsal spines; anteroventral margin with pterygostomic spine and about 21 denticles. Supraorbital spine present. Two dorsomedial protuberances and 1 well-developed spine bent forward. Eyes now stalked.

Antennule (Fig. 5B). Peduncle 3-segmented, first segment with 1 conspicuous medial spine, stylocerite forming on proximal external margin of first segment, 19 setae on distal external margin and 2 distal internal setae. Second segment with 8 setae on distal external margin and 3 internal setae. Third segment with large external seta, small medial distal lobe with 4 setae, and 2 internal setae. Exopod with 2, 3, 1, 4 aesthetascs, large distal external seta and small internal one.

Antenna (Fig. 5C). Exopod (scaphocerite) unsegmented, with well-developed external spine, 1 medial seta on outer margin, 36–38 marginal setae on distal margin (including tip). Endopod with 2 subterminal and 1 terminal small setae; ventral spines shorter than in first stage.

Mandible (Fig. 5G). Unchanged.

Maxillule: Coxal endite with 23–25 plumodenticulate setae. Basial endite with 22 spines and 6 setae. Palp 3-segmented, with 2, 2, 3 setae, respectively, external setae of first segment reduced.

Maxilla: Proximal endite of coxa with about 28 setae, distal endite small, bearing 4 setae; proximal basal endite with 12 marginal and 1 lateral setae; distal basal endite with 12 marginal setae and large one near base of palp. Palp unchanged. Exopod (scaphognathite) with 42–44 marginal plumose setae and 2 terminal flagella with long setules.

Maxilliped 1 (Fig. 5E). Coxa and basis with 12 and 40–42 plumodenticulate setae, respectively. Endopod 4-segmented, with 3+0, 2+0, 2+2, 2+1 (2 terminal, 1 subterminal) setae, respectively. Exopod with 14 long plumose natatory setae. Epipod present.

Maxilliped 2 (Fig. 5F). Coxa and basis with 3 and 13 setae, respectively. Endopod 5-segmented, with 3+2, 2+1, 0+2, 2+2, 6+1 (6 terminal, 1 subterminal) setae, respectively. Exopod with 26 long plumose natatory setae. Epipod present.

Maxilliped 3 (Fig. 5H). Coxa and basis with 0 and 5 plumodenticulate setae, respectively. Endopod 5-segmented, with 2+0, 1+1,

1+1, 4+3, 5+1 (5 terminal, 1 short subterminal) setae, respectively; exopod with 30 long plumose natatory setae. Epipod present.

Pereiopods (Fig. 5I–M). Pereiopods 1 and 2, basis with 4 setae; endopod 5-segmented, with 2+0, 1+1, 1+1, 2+2, 1+2 (2 terminal, 1 subterminal) plumodenticulate setae, respectively; exopod with 28 long plumose natatory setae. Pereiopod 3, basis with 3 setae; no other differences to pereiopods 1 and 2. Pereiopods 4 and 5, endopod unsegmented, with 2 terminal and 3 subterminal plumodenticulate setae. Exopod unsegmented, unarmed.

Abdomen (Fig. 5A). Posterior dorsal margins of somites less expanded than in first stage. Somite 6 continuous with telson.

Telson (Fig. 5D). Median indentation less pronounced than in zoea I. One new short pair of processes (now 8 pairs) at inner posterior margin. No indication of uropods.

Campylonotus capensis Bate, 1888

Zoea I.—(Fig. 6): TL = 7.4 ± 0.04 mm; CL = 2.0 ± 0.01 mm; $n = 7$.

Cephalothorax (Fig. 6A, B). Rostrum straight, without spines; anteroventral margin with pterygostomic spine and 21–23 denticles; 2 dorsal protuberances. Eyes sessile.

Antennule (Fig. 6G). Peduncle unsegmented, with 1 inner distal plumose seta. Endopod absent. Exopod unsegmented, with 4 aesthetascs and 1 subterminal plumose seta.

Antenna (Fig. 6D). Biramous. Protopod unsegmented, with 1 well-developed spine at inner distal end and 1 shorter terminal central spine. Endopod unsegmented, with 1 long apical plumose seta. Exopod (scaphocerite) with 10 terminal plumose setae and 1 long plumose medial seta.

Mandible (Fig. 6E). Well-developed molar and incisor processes; with lacinia mobilis. Palp absent.

Maxillule (Fig. 6F). Coxal endite with 24–26 plumodenticulate setae. Basial endite with 8 spines and 6 plumodenticulate setae. Endopod 2-segmented, proximal segment with 2 plumodenticulate setae, distal segment with 3 apical setae. Two simple setae at base of endopod. Exopod absent.

Maxilla (Fig. 6H). Proximal endite of coxa with 26–30 setae, distal endite small, bearing 4 setae; basal endites with 12 and 18 proximal and distal setae, respectively; palp with indications of 5 segments, partial division between first and second, complete division between second and third, segments with 3, 2, 1, 2, and 2 setae from proximal to distal, respectively; exopod with 30 or 31 marginal plumodenticulate setae and terminal flagellum with long setules.

Maxilliped 1 (Fig. 6I). Coxa and basis with 8 and 27 medial plumodenticulate setae, respectively. Endopod 4-segmented, with 14 plumodenticulate setae, arranged 3+2, 1+1, 2+1, 3+1 (3 terminal, 1 subterminal). Exopod unsegmented, with 14 long terminal plumose natatory setae. Epipod present.

Maxilliped 2 (Fig. 6K). Coxa with 2 plumodenticulate setae. Basis with 9 medial plumodenticulate setae, arranged 3, 3, 3. Endopod 5-segmented, with 18 plumodenticulate setae, arranged 2+2, 2+1, 0+1, 2+2, 5+1 (5 terminal, 1 subterminal). Exopod with 22 long terminal plumose natatory setae. Epipod present.

Maxilliped 3 (Fig. 6J). Coxa and basis with 0 and 4 plumodenticulate setae, respectively, arranged 2, 2. Endopod 5-segmented, with 17 plumodenticulate setae, arranged 2+0, 1+1, 1+1, 4+3, 3+1 (3 terminal, 1 subterminal). Exopod unsegmented, with 24 long terminal plumose natatory setae. Epipod present.

Pereiopods (Fig. 6L–P). Pereiopod 1, endopod 5-segmented; segments 1–3 with 1+0, 1+0, 1+1 plumodenticulate setae, respectively; propodus with 2 distal setae and 2 plumose setae on developing finger; dactylus with 3 apical setae; exopod without setae. Pereiopod 2, endopod 5-segmented, segments 1–3 with 0+0, 1+0, 1+0 plumodenticulate setae, respectively; propodus with 2+2 plumose setae, dactylus with 3 terminal plumose setae; exopod without setae. Pereiopod 3, endopod unsegmented, with 2 subterminal and 1 terminal setae; exopod slightly longer than endopod. Pereiopod 4, biramous; endopod with 1 terminal seta. Pereiopod 5, biramous, rudimentary.

Abdomen (Fig. 6B). First somite with anterior and posterior margins smooth, not expanded. Somites 2–5 with posterior dorsal margins expanded; fifth somite with large, ventral, smooth spine on each side. Ventral and posterior dorsal margins of all somites (except dorsal margin of first) fringed with denticles; fine setae on dorsal surface. Somite 6 continuous with telson. No trace of pleopods.

Telson (Fig. 6C). Triangular, with medial cleft and 7 pairs of processes on posterior margin.

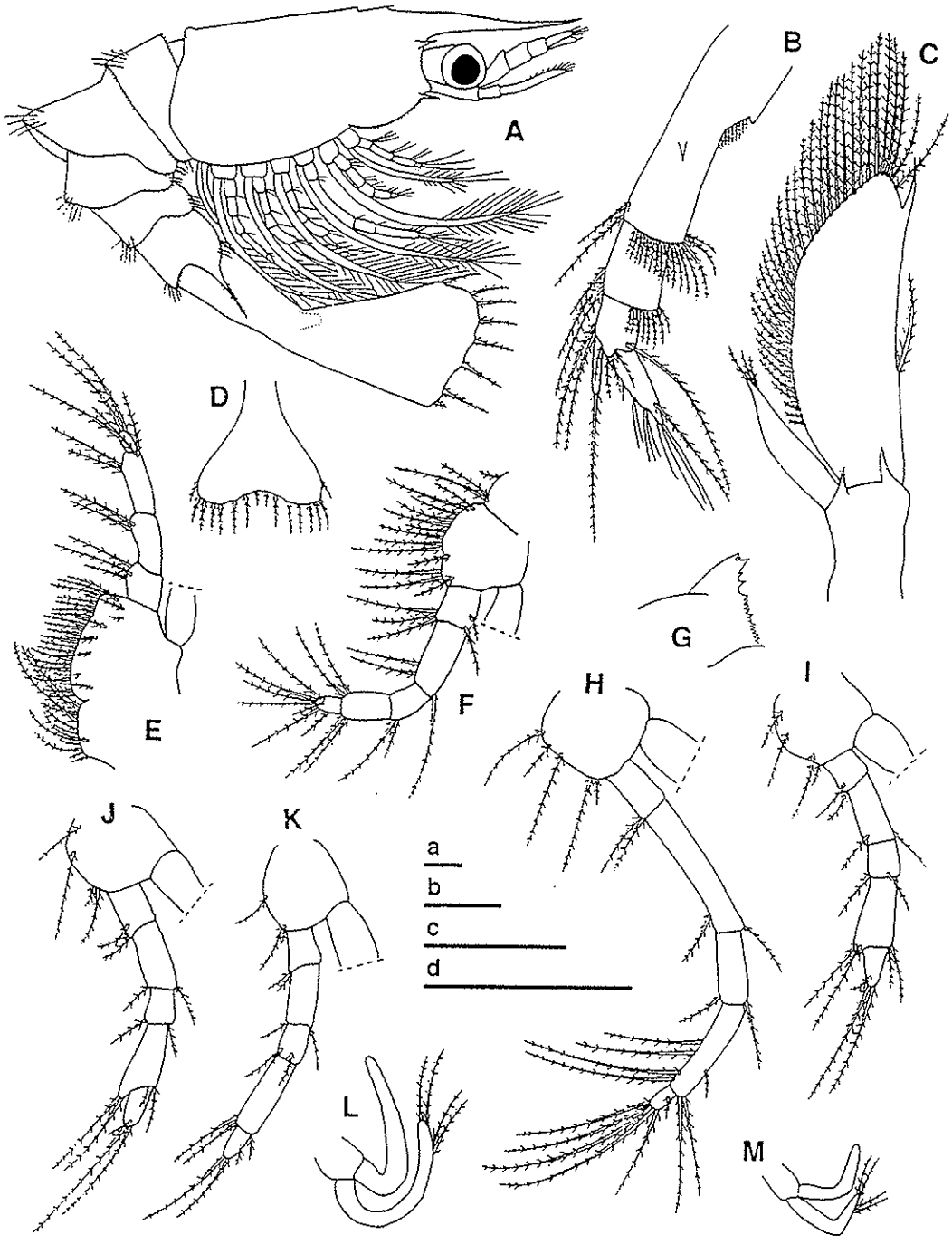

Fig. 5. Second zoeal stage of *Campylonotus semistriatus;* A, whole animal, lateral view; B, antennule; C, antenna; D, telson, ventral view; E, maxilliped 1, lateral view; F, maxilliped 2, lateral view; G, mandible; H, maxilliped 3, lateral view; I, pereiopod 1, lateral view; J, pereiopod 2, lateral view; K, pereiopod 3, lateral view; L, pereiopod 4, lateral view; M, pereiopod 5, lateral view. Scale bars: a–d = 1 mm; a (Fig. D), b (Fig. A), c (Figs. L, M), d (Figs. B, C, E–K).

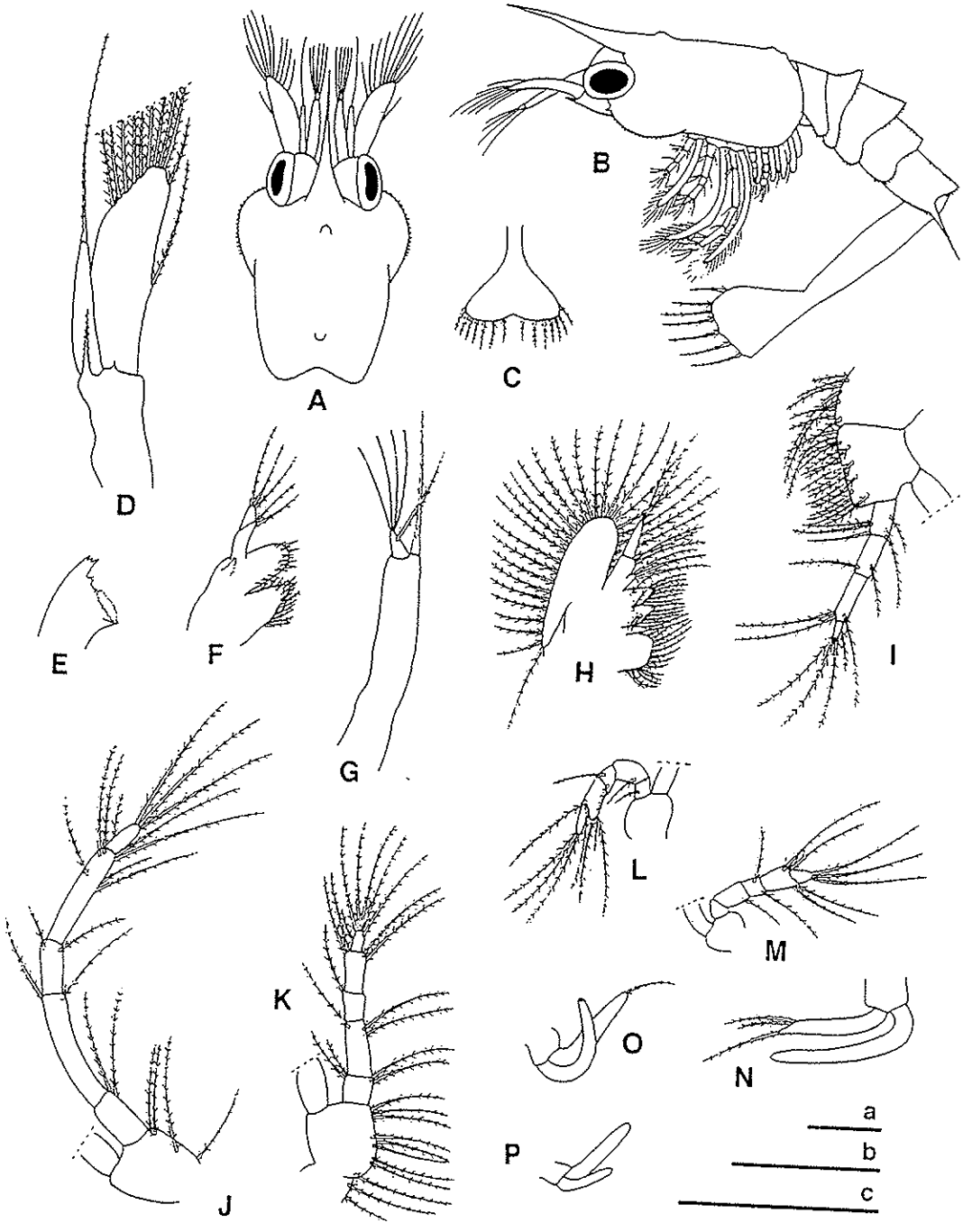

Fig. 6. First zoeal stage of *Campylonotus capensis;* A, carapace, dorsal view; B, whole animal, lateral view; C, telson, ventral view; D, antenna; E, mandible; F, maxillule; G, antennule; H, maxilla; I, maxilliped 1; J, maxilliped 3; K, maxilliped 2; L, pereiopod 1, lateral view; M, pereiopod 2, lateral view; N, pereiopod 3, lateral view; O, pereiopod 4, lateral view; P, pereiopod 5, lateral view. Scale bars: a = 2 mm (Fig. D), b = 2 mm (Figs. A, B); c = 1 mm (Figs. D–P).

KEY TO ZOEAL STAGES I AND II OF THE CAMPYLONOTIDAE FROM THE MAGELLAN REGION

1. Eyes sessile, pereiopods less developed, rudimentary; carapace with anterior and posterior dorsal protuberance; telson with 7+7 distal setae . . . . . zoea I, 2
– Eyes stalked, pereiopods 1–5 developed, telson with 8+8 distal setae . . . . . zoea II, 4
2. No pterygostomic spines; rostrum without dorsal spines; somites without expansions and setation; abdominal somite 5 with short pair of lateral spines . . . . . *Campylonotus vagans* (zoea I)
– Pterygostomic spines present; somites with expansions; abdominal somite 5 with pair of long lateral spines 3
3. Rostrum elongated, with 15 small dorsal spines; first abdominal somite with dorsal margin anteriorly and posteriorly expanded; abdominal somites 2–5 with dorsal margin posteriorly expanded, but not anteriorly, somites with setation . . . . . *Campylonotus semistriatus* (zoea I)
– Rostrum without dorsal spines; first abdominal somite without expanded margins; abdominal somites 2–5 with expanded margins, somites ornamented with denticles . . . . . *Campylonotus capensis* (zoea I)
4. Rostrum with 9 dorsal spines; anteroventral margin of carpace with pterygostomic spine and denticles; subraorbital spines present; 2 dorsomedial protuberances and 1 dorsal spine at base of rostrum well developed, directed anteriorly; abdominal somites 2–5 with dorsal margin expanded posteriorly, not anteriorly; abdominal somite 5 with long spine at both lateral sides; dorsal and ventral margins of somites ornamented with denticles; large, fine feathered setae on ventral and dorsal surface . . . . . *Campylonotus semistriatus* (zoea II)
– Abdominal somites 1–5 without posteriorly expanded dorsal margins and without denticles; somite 5 with shorter lateral spine on each side; rostrum with 2 dorsal spines at base . . . . . *Campylonotus vagans* (zoea II)

DISCUSSION

Caridean larvae show a great variability in number of larval stages and development (Fincham, 1979a, b; Criales and Anger, 1986; Villamar and Brusca, 1988; Thatje and Bacardit, 2000a). Consequently, observations on larval development in culture are very difficult, which explains the scarce number of complete descriptions from this decapod group (Wehrtmann and Báez, 1997).

Descriptions of caridean larvae separated from plankton samples are one way to extend the limited knowledge of larval development, but this method hardly allows a complete description of the larval cycle. In our case, campylonotid larvae obtained from various investigations in Magellanic waters serve as an ideal basis for first larval descriptions and more detailed studies in the future. The partial geographical separation of campylonotid species in the southernmost region of America and the confirmation of the first zoeal stage of *C. vagans* with larvae hatched in the laboratory, allows unambiguous identification of the species of the larvae studied.

The zoea I larvae described in this work are different from that of *C. rathbunae* published by Pike and Williamson (1966; Table 1). Of all four species of the Campylonotidae, *C. capensis* shows the most developed zoea I, as shown by the well-developed pereiopods 1 and 2 and the presence of setae on pereiopods 1 to 4, though the three last pairs are not segmented yet. Morphologically, the first zoea of *C. rathbunae* described by Pike and Williamson (1966) seems to be closely related to that of *C. vagans*, mainly due to the absence of pterygostomic and rostral spines and the absence of expansions on the abdominal somites in both species (Table 1). On the other hand, abdominal expansions and the presence of pterygostomic spines relate first zoeae of *C. capensis* to that of *C. semistriatus* (Table 1). Zoeae II of the examined species (*C. vagans, C. semistriatus*) are quite advanced, resembling very much the features of adults (compare with Retamal, 1981).

Although adults of *C. vagans* are very common within the Magellan region and have a wide distribution pattern (Torti and Boschi, 1973; Gorny, 1999), larvae of this species were rare in plankton samples. Monthly

Table 1. Morphological differences between zoeae I of the Campylonotidae.

	C. rathbunae	*C. capensis*	*C. semistriatus*	*C. vagans*
Dorsal rostral spines	–	–	+	–
Pterygostomic spines	–	+	+	–
Dorsal protuberances on carapace	–	+	+	+
Expansions on first abdominal segment	–	–	+	–
Setae on exopods of maxillipeds 1–3	8-16-18	14-22-24	14-16-26	9-14-17
Setae on endopods of pereiopods 1–5	+,+,0,0,0	+,+,+,+,0	+,+,+,0,0	+,+,+,0,0

– absent; + present.

plankton catches were carried out in the southwestern Atlantic Ocean from April 1978 to April 1979, but generally campylonotid larvae occurred only in samples from September to October 1978. These observations could assume an abbreviated and probably rapid development with a shortened planktonic larval phase of campylonotid larvae. First zoeae of *C. vagans* hatched in the laboratory showed a strong demersal behaviour, which may explain the absence of a more developed zoeal stage in plankton catches, as well as it supports the assumption of an abbreviated larval development. However, campylonotid larvae need at least a third zoeal stage to acquire a telson with elongated uropods typical for a late caridean larval stage. However, these assumptions must be checked in future laboratory culturing of campylonotid larvae.

Pike and Williamson (1966) compared zoeae of *C. rathbunae* with those of the families Pandalidae, Palaemonidae, and Oplophoridae. According to those authors, the long slender rostrum, the fringes of denticles on the carapace and abdominal somites, the shape of the mandible, and the presence of a long exopod on the third maxilliped are characters that zoeae of *C. rathbunae* share with some of the Pandalidae. These similarities occur also with respect to the larvae of *C. semistriatus, C. vagans,* and *C. capensis.*

Although the structure of the antennal flagellum of the zoeae I of *Campylonotus* is similar to that described for some Palaemonidae (see: *Palaemon elegans, P. longirostris, P. serratus;* Fincham, 1977, 1979b, 1983), the other characters relating zoeae of both families, such as supraorbital and pterygostomic spines, absence of external seta on the maxillule, shape of first antenna, and well-developed lateral spines on the fifth abdominal somite, are also present in some members of other families of Caridea, such as the Pandalidae (e.g., *Pandalus jordani,* see Rothlisberg, 1980; *Austropandalus grayi,* see Thatje and Bacardit, 2000b), and the Hippolytidae (e.g., *Spirontocaris spinus, Spirontocaris lilljeborgii,* see Pike and Williamson, 1961; *Latreutes laminirostris,* see Kim and Hong, 1999). Pike and Williamson (1966) pointed out that although larvae of *C. rathbunae* resemble zoeae of Pandalidae, the structure of the appendages is very similar to those of Oplophoridae, basically for the presence of four well-developed endites on the maxilla, exopods on all pereiopods, and absence of external setae on the maxillule (e.g., *Acanthephyra purpurea,* see Williamson, 1962; see also Kemp, 1907). Williamson (personal communication) remarks that these characters are more important from a phylogenetical point of view and that the presence of two coxal endites in the maxilla discards all close relations between the Campylonotidae and the Palaemonidae.

Relations between adult forms of species of this family are also subject to discussion. Borradaile (1907) and Balss (1957) grouped campylonotid species along with Oplophoridae, whereas Holthuis (1955) put them together with the Palaemonidae and Gnatophyllidae within the superfamily Palaemonoidea.

The presented larval morphology of the three additional campylonotid species supports considerably the proposed relations to the Oplophoridae as stated by the two former authors.

Acknowledgements

The authors' thanks are due to Drs. E. E. Boschi and W. E. Arntz for their great support of this work, and to Dr. I. Wehrtmann and two anonymous reviewers for their constructive comments on the manuscript. Special thanks of the second author are due to Dr. D. I. Williamson for his suggestions and discussions on the theme during the time of her thesis. The "Instituto Nacional de Investigación y Desarrollo Pesquero" (INIDEP) provided part of the plankton samples. Scientific work of the first author in South America was supported by the International Bureau of the German Ministry of Research (BMBF, project No. CHLC1A1A). This is Alfred Wegener Institute publication No. 1623.

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RECEIVED: 17 September 1999.
ACCEPTED: 17 August 2000.

ELSEVIER

Journal of Experimental Marine Biology and Ecology
301 (2004) 15–27

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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Egg production, hatching rates, and abbreviated larval development of *Campylonotus vagans* Bate, 1888 (Crustacea: Decapoda: Caridea), in subantarctic waters

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Received 1 January 2003; received in revised form 23 May 2003; accepted 1 September 2003

Abstract

Early life history patterns were studied in the caridean shrimp, *Campylonotus vagans* Bate, 1888, from the subantarctic Beagle Channel (Tierra del Fuego). As a consequence of very large egg size (minimum 1.4 mm), fecundity was low, ranging from 83 to 608 eggs per female (carapace length [CL] 11–22.5 mm). Egg size increased continuously throughout embryonic development, reaching prior to hatching about 175% of the initial diameter. Due to low daily numbers of larval release, hatching of an egg batch lasted for about 2–3 weeks. The complete larval and early juvenile development was studied in laboratory cultures fed with *Artemia* sp. nauplii. At 7.0 ± 0.5 °C, development from hatching to metamorphosis lasted for about 6 weeks. It comprised invariably two large zoeal stages and one decapodid, with mean stage durations of 12, 17, and 15 days, respectively. Larvae maintained without food survived on average for 18 days (maximum: 29 days), but did not reach the moult to the zoea II stage. Size increments at ecdysis were low in all larval stages (2.1–3.9%), indicating partial utilisation of internal energy reserves. A clearly higher increment (14%) was observed in the moult from the first to the second juvenile stage. Low fecundity, large size of eggs and larvae, an abbreviated mode of larval development, high larval survival rates during absence of food, demersal behaviour of the early life history stages, and an extended hatching period with low daily release rates are interpreted as adaptations to conditions typically prevailing in subantarctic regions, namely low temperatures (causing long durations of development) in

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doi:10.1016/j.jembe.2003.09.010

combination with a pronounced seasonality in plankton production (i.e., short periods of food availability).

Keywords: Abbreviated larval development; Decapoda; Fecundity; Hatching; Mortality

1. Introduction

Several species of caridean shrimps have developed strong life history adaptations to both latitudinally changing conditions of food and temperature (for reviews, see Clarke, 1982, 1987, 1993a). Among the most conspicuous adaptations, this includes an increasing egg size with increasing latitude and decreasing average water temperature, associated with changes in the biochemical composition of eggs, and often reduced fecundity (Gorny et al., 1992; Wehrtmann and Kattner, 1998; Wehrtmann and Lardies, 1999; Anger et al., 2002). As an additional latitudinal trend, larval size at hatching appears to increase, while the number in larval instars and the degree of morphological variability tend to decrease (cf. Wehrtmann and Albornoz, 1998; Thatje and Bacardit, 2000). Low temperatures at high latitudes have been observed to enhance not only larval development time, but also slower growth and lower mortality as compared with boreal species (Clarke and Lakhani, 1979; Arntz et al., 1992; Gorny et al., 1993).

The diversity of decapod crustaceans is comparably low in polar regions (Yaldwyn, 1965; Abele, 1982; Briggs, 1995). In the caridean shrimps, there is a strong decline in species diversity from the subantarctic (Gorny, 1999) to Antarctic waters (see Yaldwyn, 1965; Kirkwood, 1984; Tiefenbacher, 1990), with only five representatives remaining on the high Antarctic Weddell Sea shelf (Gorny, 1999).

The family Campylonotidae consists of four known subantarctic and one Antarctic representative (Gorny, 1999; Thatje, 2003). The species of this family show a wide bathymetric distribution, ranging from the shallow sublittoral to the deep sea (Thatje and Lovrich, 2003). Within the subantarctic Magellan Region (South America), the two species *Campylonotus vagans* Bate, 1888, and *Campylonotus semistriatus* Bate, 1888, are known to occur in the Argentine Beagle Channel (54°53 S, 68°17 W, Fig. 1). *C. vagans* is associated with the shallow sublittoral fauna and can be found as by-catch of the dominating galatheid crab *Munida subrugosa* (Pérez-Barros et al., in press; Tapella et al., 2002). *C. semistriatus* Bate, 1888, in contrast, is more abundant in the sublittoral below 100 m depth (Wehrtmann and Lardies, 1996).

Little is generally known about the early life history of campylonotid shrimps. Protandrous hermaphroditism is assumed to be a typical trait in this family (Yaldwyn, 1966; Torti and Boschi, 1973), but this has not been confirmed for all species. The Campylonotidae shows apparently an abbreviated mode of larval development (Pike and Williamson, 1966; Thatje et al., 2001). However, a complete description of larval and early juvenile morphology is only available for *C. vagans* (Thatje et al., 2001; Thatje and Lovrich, 2003).

The knowledge of early life history patterns in shrimps from high latitudes and, in particular, from subantarctic waters, is scarce. In the present study, we document

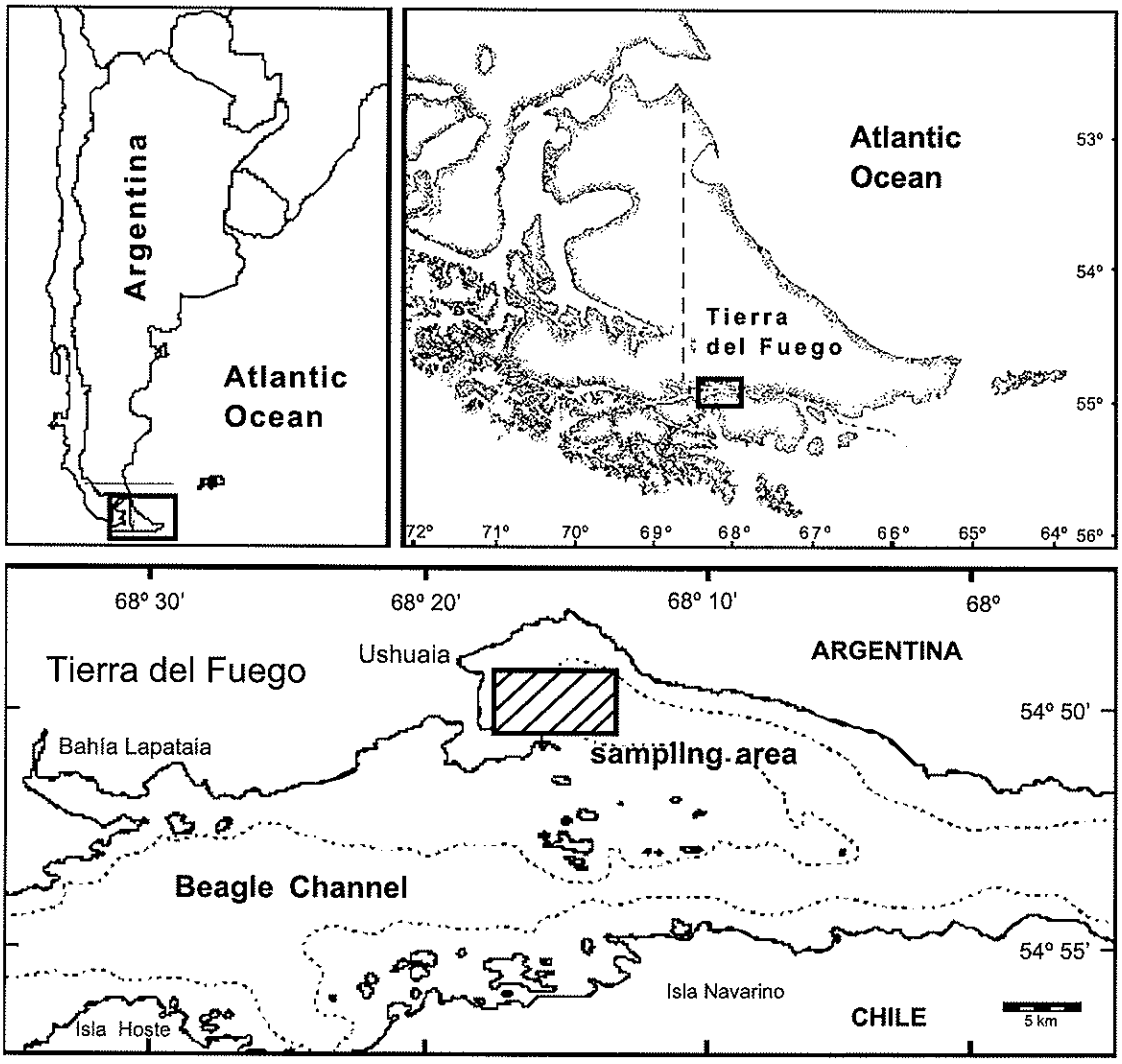

Fig. 1. Sampling location of *C. vagans* in the subantarctic Beagle Channel, South America.

laboratory observations on fecundity, egg size, hatching, as well as on larval and early juvenile development in the caridean shrimp *C. vagans* from subantarctic waters. The early life history of this species is discussed in relation to ecological conditions prevailing in the cold to temperate subantarctic region of South America.

2. Materials and methods

2.1. Sampling of ovigerous females

Ovigerous *C. vagans* were caught in September 2001 from about 15 to 30 m depth in the Beagle Channel (54°53′ S, 68°17′ W, Fig. 1) using an inflatable dinghy equipped with an epibenthic trawl (1.7 m mouth width, net with 1 cm mesh size), which was especially designed to be operated from a small boat (Tapella et al., 2002). Additional egg-carrying

females (fixed in 3–4% formalin buffered with hexamethylenetetramine) were obtained from bottom trawls taken during the expedition "Cimar Fiordo III" on board the Chilean vessel "Vidal Gormaz" to the Magellan region, the Straits of Magellan (53 °S) and the Beagle Channel (55 °S) in October 1997 (Thatje and Mutschke, 1999). Both regions show a comparable temperature regime ranging from about 4 to 9 °C in winter and summer, respectively (Lovrich, 1999; Tapella et al., 2002).

2.2. Maintenance of ovigerous females

Maintenance of ovigerous 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 (30 ‰), and a 12:12 h light/dark rhythm. The ovigerous shrimps were kept individually in tanks (minimum 30 l water content) with permanent seawater flow from a closed circulation filter system. Food (commercial TETRA AniMin pellets for aquaristics, TetraWerke, Germany) was given twice a week.

2.3. Rearing of larvae and juveniles

Hatched larvae were sampled each 24 h and collected 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. They were checked daily for dead or moulted individuals. Every second day, water was changed and food (*Artemia* sp. nauplii; Argent Chemical Laboratories, USA) was supplied. In an additional rearing, larvae from the same female ($N=48$) were kept under starvation condition.

The appearance of exuvia and visual observation of conspicuous morphological differences were used to distinguish between the different stages of larval and juvenile development. The zoea II can be easily distinguished from the previous stage by the presence of well-developed external uropods (see Thatje et al., 2001), while the decapodid is characterised by fully developed pereiopods bearing reduced exopods and complete formation of the telson (Thatje and Lovrich, 2003).

2.4. Estimation of fecundity, measurements of eggs and larvae

The term fecundity is herein considered as the number of eggs per clutch. For the calculation of clutch size/number of eggs, pleopods with attached eggs were removed from each female by cutting the pleopodal base. Eggs were directly enumerated, due to low fecundity in *C. vagans*. Fecundity in the individually kept females for the study of hatching patterns and larval development was inferred from the daily number of hatched larvae and egg losses.

The embryonic state of the eggs was divided into five stages; the first three were classified according to the criteria provided by Wehrtmann and Kattner (1998): 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. Additionally, two later developmental stages were distinguished: stage IV: eggs elongate,

Table 1
Average egg lengths of developing embryos (stage I to V, $N=25$ each) of *C. vagans* from the subantarctic Beagle Channel, South America

	Egg length (mm)	S.D.
Stage I	1.40	0.05
Stage II	1.45	0
Stage III	1.60	0.05
Stage IV	1.65	0.10
Stage V before hatching	2.45	0.05

appendages free, prezoea close to hatching; stage V: strongly elongate, appendages free, not covered by the abdomen anymore, setae of tail fan elongate. Stage V eggs were released from the female pleopods during the hatching of larvae.

After fixation of larvae in 4% buffered formalin, larval carapace length (CL) and total length (TL) were measured from the base of the rostrum between the eyes to the posterior dorsal margin of the carapace, and to the posterior margin of the telson, respectively. All lengths in eggs ($N=25$ in each stage) and larvae (see Table 2) were measured to the nearest 0.05 and 0.01 mm, respectively, using an eyepiece micrometer and a Zeiss stereomicroscope.

2.5. Statistical treatments

The relationship between fecundity and female size was analyzed with a linear regression analysis (Sokal and Rohlf, 1995) previously log-transforming data to achieve linearity.

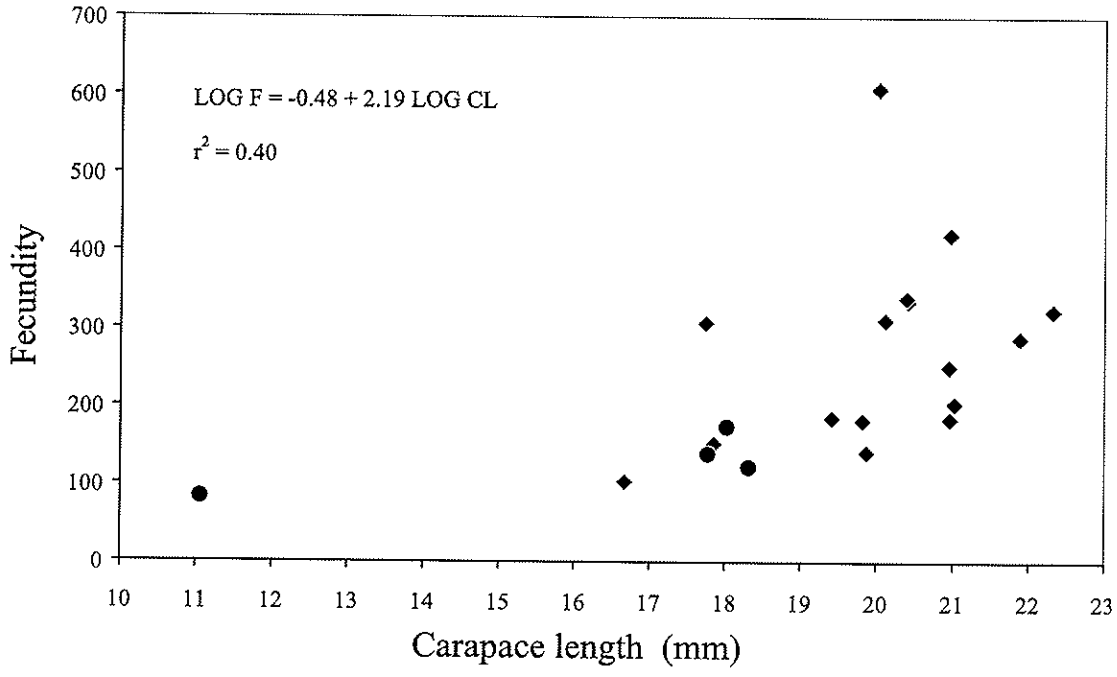

Fig. 2. Female fecundity in *C. vagans* from the subantarctic Beagle Channel, South America. Round dots indicate females maintained for larval development studies.

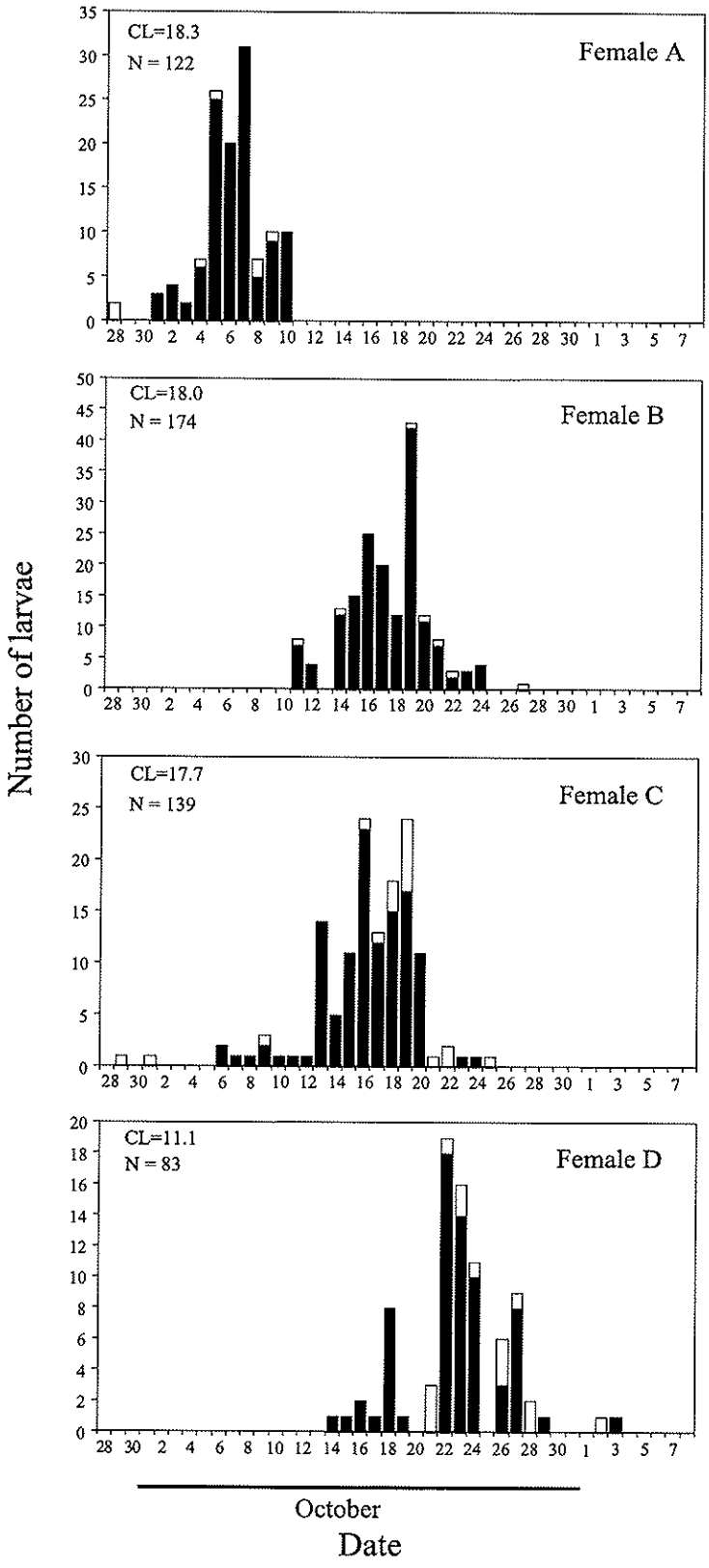

Fig. 3. Daily hatching rates in *C. vagans* from the subantarctic Beagle Channel in 2001. Bare bars represent the egg losses.

Significant differences in egg sizes among the different stages were tested using a one-way ANOVA (Sokal and Rohlf, 1995). Assumptions of homoscedasticity and normality were tested with Bartlett's and Kolmogorov–Smirnov tests, respectively. For the ANOVA, we pooled the egg size data of stages I and II because of strong similarity and no variability in stage II (Table 1).

3. Results

3.1. Fecundity and developmental increase in egg sizes

Fecundity of *C. vagans* from the Beagle Channel was low, varying from 83 to 608 eggs per female ($N=20$, Fig. 2). In spite of high individual variability, the log number of eggs increased significantly with log female size, and followed the linear function: log N eggs $=2.2$ log LC -0.5 (Fig. 2; $F_{\text{regress}}=13.5$; $P=0.002$).

During embryonic development from stages I to IV, we observed a continuous increase in egg size (Table 1). Eggs prior to hatching (stage V) were significantly larger than those in earlier stages (stages I+II combined; $F=9061.7$; $P<0.001$), reaching eventually 175% of the initial (stage I) size.

3.2. Hatching pattern and larval development

The first larvae hatched at night, about a fortnight after the capture of ovigerous females, showing a strong demersal behaviour. Nocturnal hatching of larvae occurred through an extended period varying from 10 to 21 days. Normally, about 4–17% of the total egg clutch hatched during single nights, exceptionally up to 25% (see female A, Fig. 3). The amount of eggs lost during hatching usually corresponded to about 0–15% of the respective nocturnal hatching rate of larvae. In some cases, however, egg losses were very high, and corresponded to about 35–50% of the respective nocturnal hatching rate of larvae (females C, D, Fig. 3). In almost all cases, stage V eggs were lost, indicating prezoeae close to hatching.

The development from hatching to metamorphosis lasted about 6 weeks. It comprised two zoeal stages and one decapodid, with mean durations of 12, 17, and 15 days, respectively (Table 2). Most of this time was spent in the zoea II stage, which showed also

Table 2
Average lengths (TL, CL) and developmental times in larvae and early juveniles of *C. vagans* from the subantarctic Beagle Channel, South America

	Total length, TL	Carapace length, CL	Developmental time (days)
Zoea I	4.76 (0.09; 29)	1.18 (0.05; 29)	11.7 (0.89; 32)
Zoea II	4.86 (0.09; 13)	1.12 (0.06;13)	16.7 (4.2; 15)
Decapodid	5.15 (0.04; 21)	1.25 (0.04; 21)	15.3 (2.3; 6)
Juvenile I	5.35 (0.07; 8)	1.45 (0.07; 8)	19.5 (0.7; 2)
Juvenile II	6.1 (0.3; 2)	1.55(0.05; 2)	

In brackets: standard deviation; *N*.

the highest variability in development time (Table 2). Highest mortality was found at metamorphosis from the zoea II to the decapodid stage (about 60%), and during the subsequent moult to the first juvenile stage (67%; Fig. 4A). The larvae were large already

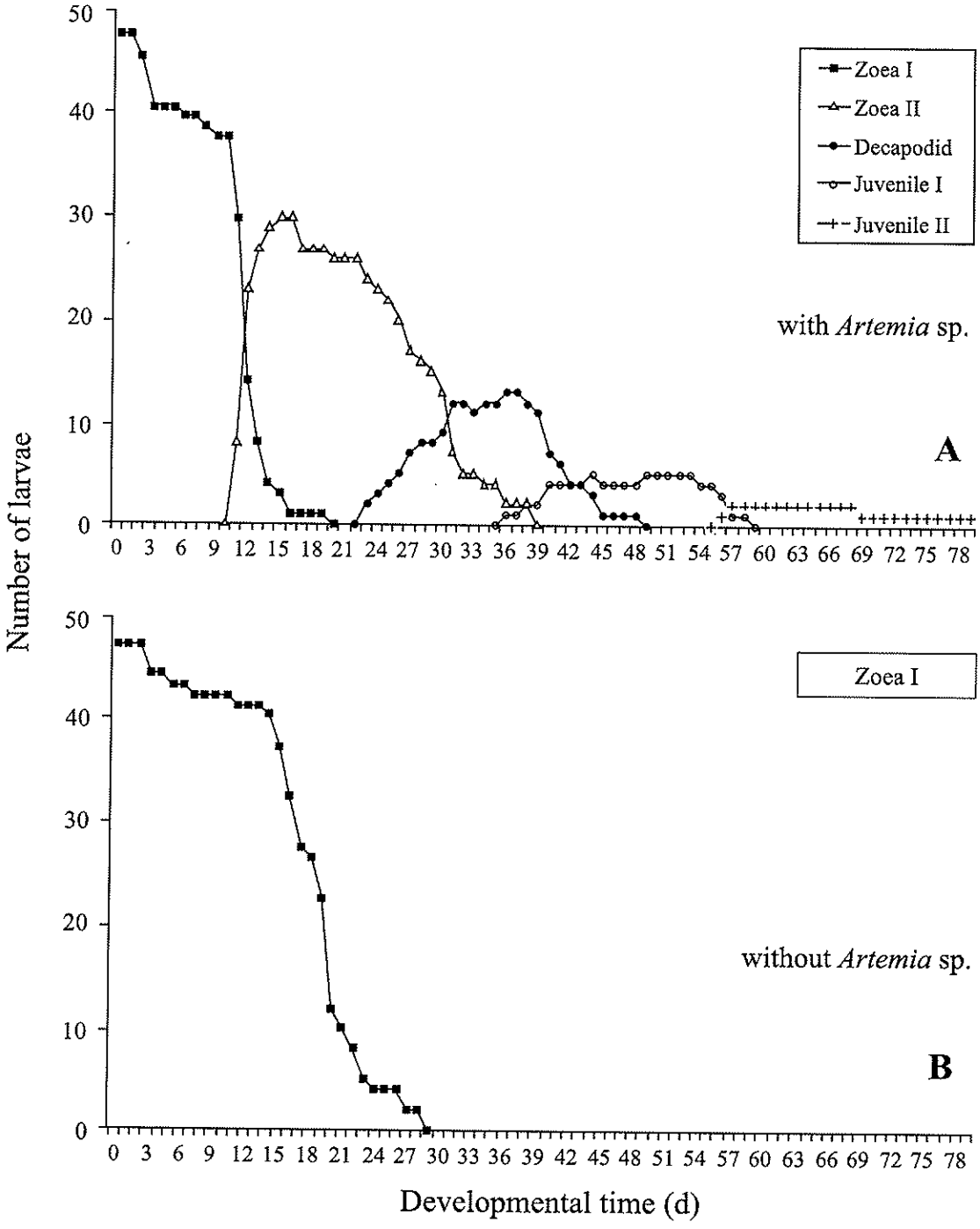

Fig. 4. *C. vagans*, changes in the number of larvae throughout larval development (A) larvae and early juveniles with food (*Artemia* sp.) and (B) zoea I without food (*Artemia* sp.).

at hatching (average TL = 4.8 mm; Table 2), but in the subsequent moults, they showed low growth rates, with TL increments of 2.1%, 3.4% and 3.9%, respectively. The moult of the first to the second juvenile stage, by contrast, was accompanied by an increment in size of about 14%.

Larvae kept under starvation conditions (without *Artemia* sp.) did not reach the moult to the zoea II stage. The average survival time lasted 18 days, although some larvae survived for up to almost 1 month (29 days), i.e., about three times longer than the average stage duration in fed zoeae (Fig. 4A,B).

4. Discussion

The Campylonotidae shows protandrous hermaphroditism, which is typical of caridean shrimps (Bauer, 1989, and references therein) and has been interpreted as an energetic life history response to low temperatures in high latitudes (Yaldwyn, 1966; Torti and Boschi, 1973). We suggest sex reversal in *C. vagans* to occur at a body size of approximately 11 mm CL, which corresponds to the size of the smallest ovigerous female found in the present study (Fig. 2). However, further investigations are needed to define exact size of sex reversal in the Campylonotidae. Most females carrying eggs had a CL of >16.5 mm (Fig. 2), and, therefore, the smallest ovigerous female found may not be representative for the population.

Extended hatching periods in decapods of high latitudes were recently discussed to be a mechanism for synchronising larval occurrence with short periods of primary production/ food availability in high latitudes (for a detailed discussion, see Thatje et al., 2003a). Extended hatching periods may also allow for avoiding predation on the small offspring (see Thatje et al., 2003a).

C. vagans showed low fecundity (compare with Reid and Corey, 1991), large eggs (Anger et al., 2002) at extrusion, and a strong increase in egg size during embryonic development (Table 1). The analyses of fecundity referred to all eggs independent of the embryonic development, due to few adult specimens available. Our fecundity estimates may therefore be biased by the high rates in egg losses during embryonic development, as demonstrated during hatching (Fig. 3). However, despite the females kept for rearing experiments of larvae, the eggs of all other preserved ovigerous females utilised had not reached the embryo stages IV to V yet. Since egg size increases dramatically in the very final stage of embryo development (Table 1), which obviously causes an increase of the entire batch, high amounts of egg losses may be typical of the hatching period only. In the final stage of embryo development, abdominal pleurae and pleopods do not cover the entire egg mass anymore, thus the less protected batch should be more sensitive to abrupt female behaviour and/or external physical impact.

Clarke (1993b) demonstrated a positive relationship between the extent of increase in egg size or volume and the level of nutrients stored in the eggs; this should indicate an enhanced female energy investment per offspring. However, egg size is not always a good indicator for nutrient contents, since nutrient contents of eggs may also be density dependent (Anger et al., 2002). From an evolutionary point of view, large larval size at

hatching is commonly associated with an abbreviated mode of larval development (Thatje et al., 2001), which is advantageous in regions with short periods of primary production. Although low temperatures affect developmental rates negatively, a reduction in the number of larval moults reduces the energetic costs for larval development (Anger, 1998; Thatje et al., 2003a; Thatje et al., in press). Microscopical observations showed that the zoea I of *C. vagans* starts feeding immediately after hatching. On the other hand, starvation experiments indicated that the resistance of unfed larvae to nutritional stress is extremely high, extending the zoea I duration up to threefold. Some larvae which survived 3 weeks of starvation ($N=6$) were re-fed and had retained the capability of reaching the moult to the subsequent zoeal stage. This indicates a very late appearance of a critical point, the point-of-no-return (Anger, 1987). This preliminary observation suggests that the zoea I of *C. vagans* contains high initial energy reserves, and recent investigation has shown that the larval energy supply in *C. vagans* mainly depends on proteins (Thatje et al., 2003b; Thatje et al., in press). These internal reserves alone, however, are insufficient to reach the moult to the zoea II stage in complete absence of food.

Larval sizes in the present study showed a clear discrepancy when compared with larvae from plankton catches obtained in the southwestern Atlantic Ocean (Thatje et al., 2001, zoea I, CL=1.9 mm, TL=5.8 mm; zoea II, CL=2.0 mm, TL=6.9 mm). These striking differences should indicate that intraspecific variability is high, and may be correlated with female fitness and size. Plasticity in caridean larval developments was shown to be responsible for changes in larval size and developmental pathways in *Nauticaris magellanica* (Thatje and Bacardit, 2000; Wehrtmann and Albornoz, 2003), being temperature dependent. In addition, differences in larval developments between laboratory reared and field collected larvae were shown to be affected by rearing conditions (Wehrtmann and Albornoz, 2003). Both patterns may help to explain the observed size differences in larvae of *C. vagans*, since the study of fatty acid contents in both larvae and *Artemia* sp. nauplii, may suggest that utilisation of the *Artemia* by larvae of *C. vagans* is not optimal (Thatje et al., 2003b; Thatje et al., in press). Despite the great intraspecific variability at hatching, this may explain the much slower growth in our laboratory reared larvae (Table 2, zoea I to zoea II, about 2.1%) when compared with previous work (zoea I to zoea II, about 19%, see Thatje et al., 2001).

In subantarctic regions, we find decapod crustacean species with both planktotrophic and lecithotrophic modes of larval development. In the former category, however, there is a tendency towards a reduction of the larval phase and an increase in initial larval size (Thatje and Bacardit, 2000; Thatje et al., 2001). More abbreviated types of larval development typically imply lecithotrophy, often associated with behavioural changes such as demersal drifting rather than active planktonic swimming. Such patterns are typical for decapods in the Magellan region (Thatje et al., 2003a), although complete lecithotrophy was, so far, experimentally demonstrated only in larvae of lithodid crabs from this region (e.g., Lovrich et al., 2003).

Future research should focus on early life histories of Antarctic shrimp species, which should be still more adapted to conditions of cold and food limitation (see Clarke, 1977, 1993b; Gorny and George, 1997). If typical reproductive adaptations result in a partial or complete food-independent larval development in high latitudes, we should expect to find

large sizes and a high initial lipid content of the eggs and larvae, an abbreviated larval development, and a high degree of endotrophy.

Acknowledgements

We are grateful to the International Bureau of the German Ministry of Research (BMBF, Project No. IB Arg 99/002) and the Argentine Secretaría Nacional para la Tecnología, Ciencia e Inovación Productiva (SETCIP) for continuous financial support of this bilateral co-operation during the last years. Thanks are due to Marcelo Gutierrez for assistance in the field. Federico Tapella provided the map on the study area. This work was partially funded by the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany. The improvements of an earlier draft by the detailed comments of two anonymous reviewers are greatly acknowledged. **[RW]**

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Journal of Experimental Marine Biology and Ecology
301 (2004) 159–174

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

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

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Received 1 May 2003; received in revised form 9 September 2003; accepted 30 September 2003

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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0022-0981/$ - see front matter
doi:10.1016/j.jembe.2003.09.019

(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.

Keywords: Abbreviated larval development; Fatty acids; Lipids; Protein; Shrimp; Southern Ocean

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

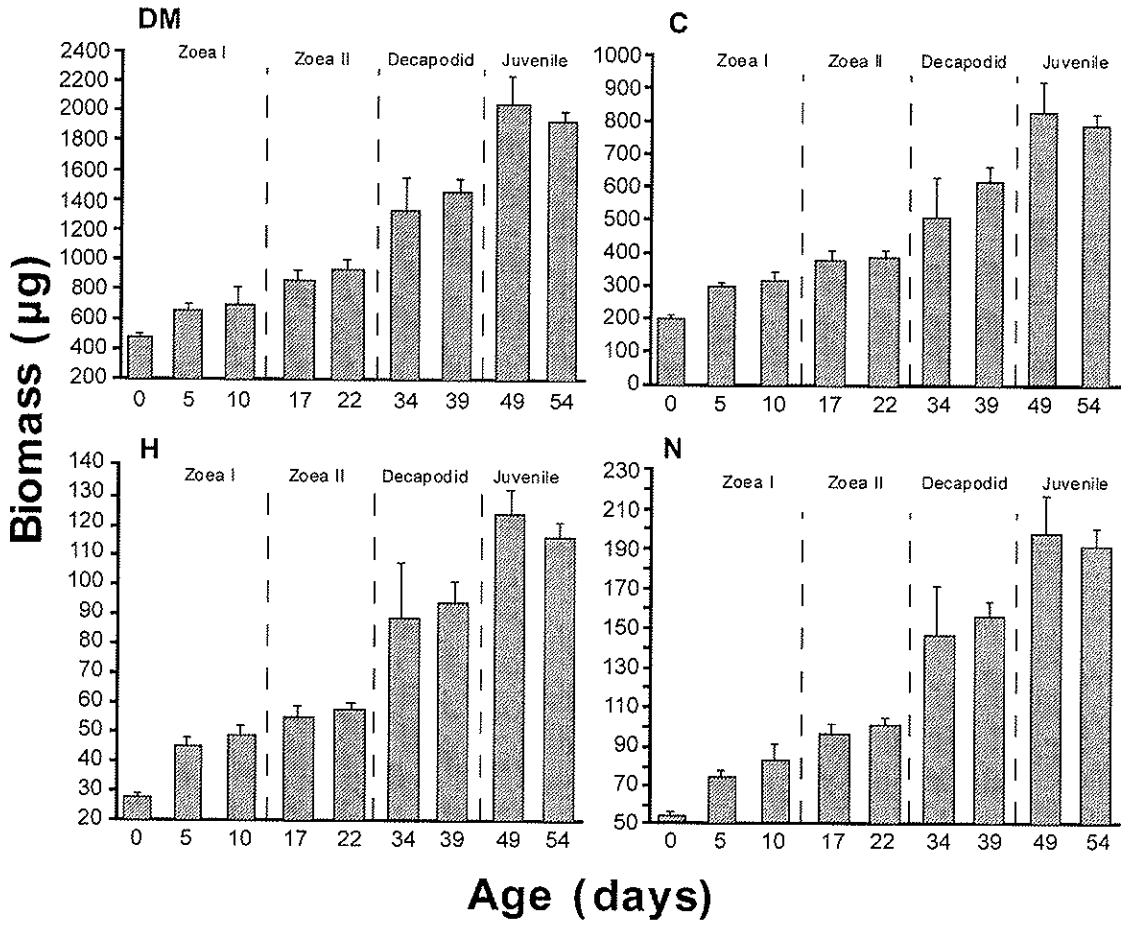

Fig. 1. *C. vagans*. Changes in dry mass (DM) and contents of carbon (C), nitrogen (N) and hydrogen (H) (all in µg/individual; $x \pm$ S.D.) during larval and early juvenile development in the presence of food (*Artemia* sp.).

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 °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; $x \pm$ 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 (μg/individual) with *Artemia*		C (%DM) with *Artemia*		N (%DM) with *Artemia*		H (%DM) with *Artemia*	
		(a)	(b)	x	±	x	±	x	±	X	±
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
	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 × 0.25 mm i.d. wall-coated open tubular column (film thickness: 0.25 μm; 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 (μg/individual) without *Artemia*		C (%DM) without *Artemia*		N (%DM) without *Artemia*		H (%DM) without *Artemia*	
			x	±	x	±	x	±	x	±
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).

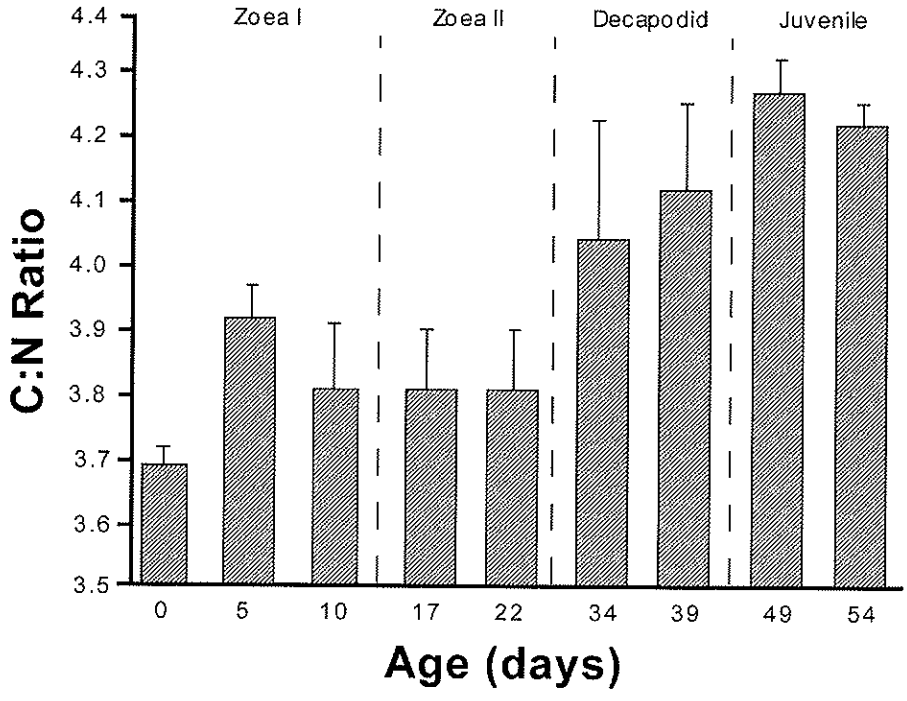

Fig. 2. *C. vagans*. Carbon/nitrogen (C:N) mass ratio during larval and early juvenile development in the presence of food (*Artemia* sp.).

Table 3
C. vagans. Parameters of linear regressions describing changes in dry mass (DM), contents of carbon (C), nitrogen (N), hydrogen (H) (all in µg/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*
With Artemia					
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
Without Artemia					
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 µg/individual and in percent of W), C:N mass ratio of the exuviae of all larval stages; $x \pm$ S.D.

Stage		N	DM		C		N		H		C:N mass ratio	
			x	±	*x*	±	*x*	±	*x*	±	*x*	±
Zoea I	µg/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	µg/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	µg/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).

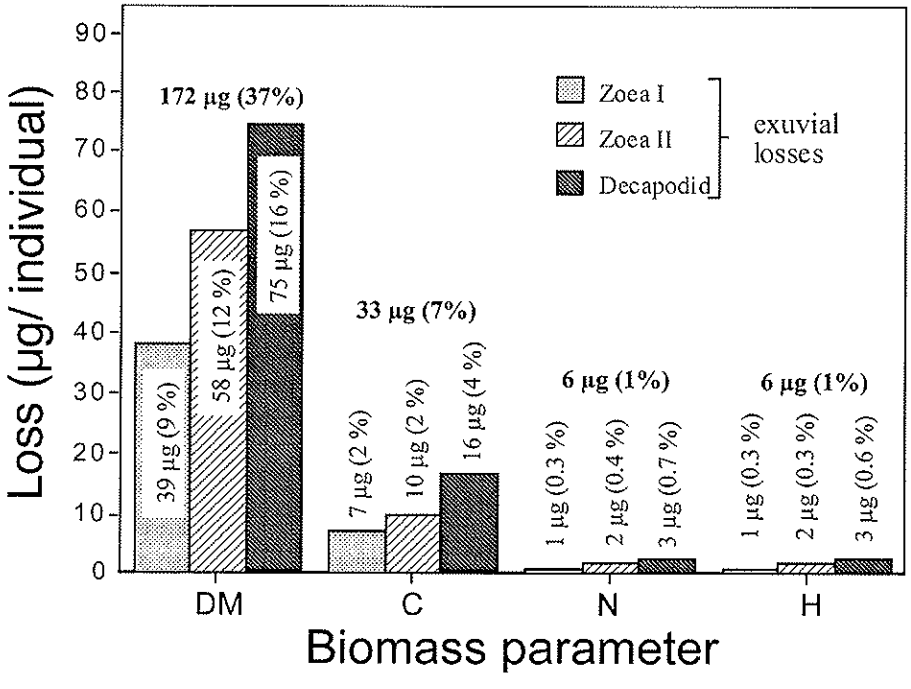

Fig. 3. *C. vagans*. Exuvial losses of dry mass (DM), carbon (C), nitrogen (N) and hydrogen (H), given in µg/ individual ($x \pm$ S.D.) and in percent of the initial biomass at hatching.

Table 5
Changes in the protein content (µg/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	µg/ind.	189.5 ± 30.7	281.3 ± 25.2	336.1 ± 37.8	388.1 ± 38.6	389.5 ± 49.1	496.1 ± 46.8	587.4 ± 65.6	642.1 ± 204.8
	%DM	38.6 ± 0.7	42.1 ± 1.6	47.5 ± 5.8	43.1 ± 2.5	41.4 ± 1.9	37.8 ± 6.5	40.6 ± 1.4	31.0 ± 1.7
B	µg/ind.	201.1 ± 21.1	280.8 ± 68.6	273.0 ± 34.3	326.5 ± 38.5	407.6 ± 56.9	479.4 ± 39.4		
	%DM	48.0 ± 6.6	46.5 ± 6.6	40.9 ± 1.6	35.9 ± 2.6	44.2 ± 5.1	37.4 ± 1.9		
C −*Artemia*	µg/ind.	229.6 ± 77.6	236.5 ± 12.0	181.1 ± 11.9					
	%DM	48.3 ± 1.5	51.9 ± 2.5	63.9 ± 2.2					
D	µg/ind.	209.3 ± 18.6							
	%DM	49.8 ± 6.9							
E	µg/ind.	191.1 ± 27.6							
	%DM	47.2 ± 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 μg/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 μg/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 μg/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	μg/ind.	37	52	64	60	63	51	37	95	70
	%DM	8	8	9	7	7	4	3	5	4
C – *Artemia*	μg/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		*Artemia* 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 intensed 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.

Acknowledgements

This project was funded by the International Bureau of the German Ministry of Research (BMBF, project no. ARG 99/002), the Argentine Secretaría Nacional para la Tecnología, Ciencia e Inovación Productiva (SETCIP), and the Alfred Wegener Institute for Polar and Marine Research, Bremerhaven, Germany. Marcelo Gutiérrez was a great help at sea and in the lab. We would like to thank Petra Wencke for her assistance in the fatty acid analyses. [SS]

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Vol. 260: 195–207, 2003 | MARINE ECOLOGY PROGRESS SERIES
Mar Ecol Prog Ser | Published September 30

Developmental trade-offs in Subantarctic meroplankton communities and the enigma of low decapod diversity in high southern latitudes

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ABSTRACT: Developmental modes, occurrence and distribution patterns of invertebrate larvae were studied in the Subantarctic Magellan region of South America on the basis of quantitative plankton hauls obtained during the 'Victor Hensen' campaign in November 1994. The meroplankton community was found to be numerically dominated by decapod crustacean larvae (47%), followed by polychaetes (20%), echinoderms (16%), cirripedes (8%) and molluscs (7%). A rich decapod community was detected, with 2 thalassinid, 5 brachyuran, 4 anomuran, 6 caridean, 1 astacid and 1 palinurid species/morphotypes identified. Cluster analyses clearly distinguished deep-water stations (250 to 400 m) south of the Straits of Magellan from shallow-water stations (30 to 100 m) in the Beagle Channel, where meroplankton was dominated by decapod larvae (>90%). Three main larval developmental modes, characterised by morphogenesis, mode of larval nutrition and site of larval development, were observed in Magellan decapods: (1) Extended, planktotrophic development of planktonic larvae; (2) abbreviated, planktotrophic development of planktonic larvae; and (3) abbreviated, endotrophic (lecithotrophic) development of demersally living larvae. Several caridean shrimps with abbreviated larval development, which have congeners in the Antarctic, suggest a strong synchronisation between abbreviated planktotrophic larval development and short periods of primary production. This seems to be an essential factor in early life history adaptation for the colonisation of the Antarctic environment. The impoverished Antarctic decapod fauna, with only a few representatives of caridean shrimp species left, may be related to the lack in flexibility of reptant decapods in distributing energy resources between adults and their offspring, which would allow abbreviated planktotrophic larval development.

KEY WORDS: Decapoda · Reproductive strategies · Southern Ocean · Abbreviated larval development · Magellan region · Antarctic

INTRODUCTION

The Southern Ocean decapod fauna still provides one of the most conspicuous unsolved mysteries in marine biodiversity research, with an Antarctic decapod fauna of only about a dozen caridean shrimp representatives compared with more than 120 benthic and pelagic decapod species in the circumpolar antiboreal environment north of the Antarctic Convergence (Gorny 1999). Apart from a few species of lithodid crabs in the deeper waters off the Antarctic continental shelf (Macpherson 1988, Klages et al. 1995, Arana & Retamal 2000), caridean shrimps represent the only decapod infraorder which endures the high Antarctic regime of very low temperatures combined with a marked seasonality of primary production (Clarke 1988).

The absence of reptant decapods, in particular brachyuran crabs, from polar environments of both hemispheres was recently discussed to be predominantly due to physiological constraints, i.e. the failure of adults to control high Mg^{2+} concentrations in their haemolymph, which in combination with low tempera-

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tures, leads to a paralysing condition affecting all kinds of behaviour (Frederich et al. 2001). However, this explanation of physiological constraints on ecological demands alone cannot explain the observed decapod biodiversity patterns, since at least lithodid (anomuran) crabs have been shown to respond to physiological constraints in the cold by life history adaptation of both adults and larvae (see Anger et al. 2003, Lovrich et al. 2003, Thatje et al. 2003). In an attempt to elucidate the reason for the impoverished decapod fauna in high latitudes, we revisited Thorson's old ecological concept (Thorson 1936, 1950), which, in summary, argues that the mismatch between a marked seasonality of primary production (i.e. food availability) and prolonged larval developmental times due to low temperatures at high latitudes, should strongly select against planktotrophic larval development (see Mileikowsky 1971, who created the term 'Thorson's rule', Clarke 1988, Pearse et al. 1991, Arntz & Gili 2001).

In this study, we present information on developmental trade-offs in early life history of benthic decapod crustaceans from the Magellan region and the position of decapod larvae within the Subantarctic meroplankton community. This information is augmented by literature data, including findings on early life history adaptation of Antarctic shrimps to a cold and seasonally food-limited environment.

MATERIALS AND METHODS

Sampling and sample treatment. Quantitative meroplankton samples were obtained during the Joint Chilean-German-Italian Magellan 'Victor Hensen' Campaign to the channel and fjord system of the cold-temperate Subantarctic Magellan region (Fig. 1) from 12 to 24 November 1994 (see also Arntz & Gorny 1996, Defren-Jansen et al. 1999). Zooplankton samples were obtained using a multiple opening-closing net of 300 µm mesh size. Daytime vertical hauls were conducted from the seafloor or 400 m maximum wire length to the surface, covering standard depth intervals (see Figs. 6 & 7). Zooplankton samples were directly preserved in 4% borax-buffered formaldehyde seawater solution, and later in the laboratory split into two. Assuming 100% filtering efficiency of the multinet for meroplankton, the filtered volume was calculated by multiplying the vertical distance of the tow by the mouth area of the net (0.25 m^2).

Species identification and larval developmental mode. The meroplankton fraction was sorted only from one part of the sample, and identified to the most resolved taxonomic level possible. Special focus was given to species determination of decapod crustacean larvae as well as their developmental stages (for literature used for larval identification see Table 2). To detect relevant developmental patterns in decapod larvae, we distinguished 3 larval developmental modes, characterised as follows (for review see Williamson 1982, Anger 2001):

(1) Morphogenesis
- Extended larval development — number of instars typical of the family/genus.
- Abbreviated larval development — comprises a considerable reduction in larval instars compared with typical trait of family/genus representatives from lower latitudes and/or intraspecific changes with latitude/temperature regime.

(2) Mode of larval nutrition
- Planktotrophic larval development — most of the larval development requires actively feeding planktonic larvae. This may include partial utilisation of energy reserves of maternal origin in an early stage of development.
- Lecithotrophic larval development — complete endotrophic larval development (complete lecithotrophy) with planktonically and/or demersally living larvae.

(3) Site of larval development
- Planktonic larval development — larval development is spent mostly in the water column.
- Demersal larval development — larval development is predominantly epibenthic.

Cluster analyses. We used the software package PRIMER (Plymouth Routines in Multivariate Ecological Research) developed at Plymouth Marine Laboratory,

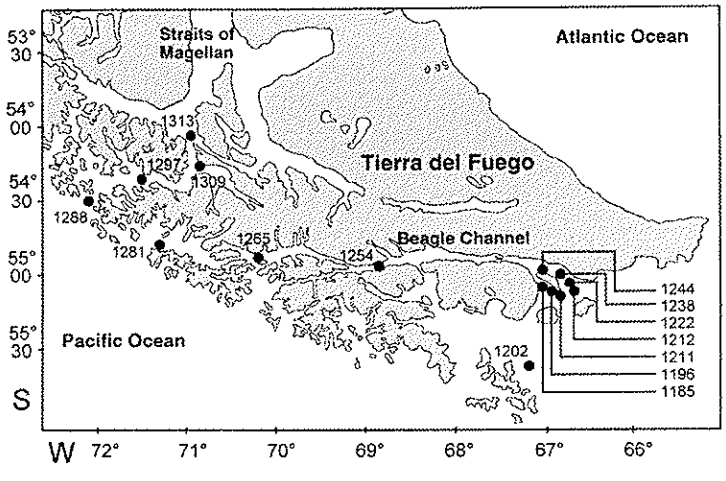

Fig. 1. Meroplankton sampling locations (black dots/station numbers) during the Joint Chilean-German-Italian Magellan 'Victor Hensen' Campaign to the Magellan region (South America) in November 1994

Table 1. Station means (ind. m^{-3}) of meroplankton taxa found in the channel and fjord system of the Subantarctic Magellan region during the Joint Chilean-German-Italian 'Victor Hensen' Campaign in November 1994 (adv. = advanced). (?) Species identification not certain

Species/group	Stage	Station (Sampling depth, m)														
		1313 (340)	1309 (250)	1297 (380)	1288 (400)	1281 (340)	1265 (400)	1254 (270)	1244 (30)	1238 (100)	1222 (30)	1212 (50)	1211 (50)	1196 (100)	1185 (100)	1202 (30)
Bryozoa	Cyphonautes	227	–	310	1240	44	47	55	7	4	13	5	–	24	4	–
Cirripedia	Nauplius	458	75	298	1291	2020	64	2445	27	108	480	10	–	468	16	53
Gastropoda	Veliger	202	25	268	1262	100	42	18	20	244	120	35	50	28	28	133
Bivalvia	Veliger	376	13	1055	2113	24	–	3	–	4	7	5	–	4	–	–
Polychaeta	Larvae	5489	1110	5093	2793	1267	298	613	120	372	193	65	5	416	248	67
Ophiuroidea	Ophiopluteus	702	65	755	1060	529	56	1370	–	–	–	–	–	–	–	–
	Juvenile	–	93	–	–	–	58	–	–	–	–	–	–	–	–	–
Asteroidea	Brachiolaria	751	25	610	564	84	–	135	–	–	–	–	–	8	–	–
Echinoidea	Echinopluteus	3051	625	2413	853	451	129	1210	–	12	–	–	–	36	–	–
Decapoda																
Thalassinidea																
Notiax sp. (?)	Zoea 1	–	–	–	–	–	–	30	1440	9224	20	35	30	6424	3756	240
	Zoea 2	–	–	–	–	–	–	–	127	3076	–	–	–	520	1808	13
Upogebia sp.	Decapodid	–	–	–	–	–	–	–	7	–	–	–	–	–	8	–
Brachyura																
Pinnotheridae	Early zoea	4	–	–	2	–	–	3	100	–	–	–	–	–	36	–
Libidoclaea granaria	Zoea 1	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–
Eurypodius latreillei	Early zoea	69	150	255	231	27	82	128	3107	304	–	80	35	504	184	–
	Adv. zoea	76	148	188	598	120	44	90	1100	68	–	40	15	68	24	–
Peltarion spinosulum	Zoea 1	–	–	13	–	–	–	13	–	4	133	–	5	4	–	147
	Zoea 2	–	–	–	–	–	7	–	–	8	33	–	–	–	–	7
Halicarcinus planatus	Zoea 1	–	–	–	36	–	–	–	53	–	–	5	–	8	12	–
	Zoea 2	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–
Anomura																
Pagurus spp.	Zoea 1	–	–	–	11	–	–	–	160	12	20	25	20	4	72	–
	Zoea 2	–	–	–	–	–	11	–	247	16	–	60	100	12	20	–
	Zoea 3	–	–	–	67	–	–	13	240	76	33	35	50	20	8	7
	Zoea 4	11	28	25	213	–	–	–	293	52	20	90	100	152	16	20
	Megalopa	–	13	–	33	–	–	–	147	20	13	10	20	36	28	47
Parapagurus dimorphus (?)	Early zoea	–	–	–	–	–	–	–	–	–	–	–	5	20	4	–
	Adv. zoea	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–
Munida spp.	Zoea 1	–	–	–	–	–	11	10	647	344	20	30	5	96	76	7
	Zoea 2	–	–	–	–	–	–	–	320	892	7	20	–	40	44	7
	Zoea 3	2	–	–	–	–	–	–	173	8	40	5	65	4	–	7
	Zoea 4	–	–	–	–	–	–	35	147	260	13	70	10	132	20	13
	Megalopa	–	–	–	–	–	–	–	80	–	7	–	–	–	–	–
Caridea																
Betaeus truncatus	Zoea 1	–	–	–	–	–	–	–	–	–	7	–	–	–	–	–
Eualus dozei	Zoea 1	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–
Campylonotus vagans	Zoea 1	–	–	–	–	–	–	–	–	–	–	10	–	–	–	–
	Zoea 2	–	–	–	–	–	–	–	–	–	–	10	–	8	–	–
	Decapodid	–	–	–	–	–	–	–	–	–	–	–	–	–	40	–
C. semistriatus	Decapodid	22	–	–	–	–	–	–	–	–	–	–	–	–	–	–
Nauticaris magellanica	Zoea 1	–	–	–	31	–	–	3	–	12	–	5	–	28	–	7
	Zoea 2	–	–	–	–	–	–	13	–	16	–	–	–	4	–	7
	Zoea 3	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–
	Zoea 4	4	–	–	–	–	–	–	–	–	–	10	–	–	–	–
	Zoea 5	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–
	Decapodid	11	–	–	22	–	–	–	–	–	–	–	–	4	–	–
Austropandalus grayi	Zoea 1	–	–	–	–	4	22	8	–	12	–	5	–	16	32	–
	Zoea 2	–	–	–	22	–	22	–	7	4	–	–	–	8	16	–
	Zoea 3	–	–	–	89	–	–	–	7	4	–	–	–	–	8	7
	Zoea 4	–	38	–	311	11	–	–	13	–	7	–	–	–	4	–
	Zoea 5	–	–	–	122	4	–	–	–	60	–	–	–	–	–	7
	Decapodid	–	3	–	111	–	13	–	–	–	–	–	10	–	4	–
Astacidea																
Thymops birsteini	Decapodid	–	13	–	–	–	22	–	–	8	–	–	–	–	–	–
Palinura																
Stereomastis (*suhmi* ?)	Early zoea	–	–	–	–	22	–	–	7	–	–	–	–	–	8	–
	Adv. zoea	–	–	–	–	22	–	–	–	–	–	10	–	–	–	–
Sum		11455	2424	11283	13075	4729	928	6195	8610	15224	1196	665	525	9108	6532	796

UK. The hierarchical agglomerate cluster method (Clarke & Gorley 2001) was applied on the basis of abundance means per station to differentiate meroplankton communities utilising the Bray-Curtis similarity index. Data were previously log(x+1) transformed to remove the bias of highly abundant taxa.

RESULTS

Meroplankton composition and distribution pattern

The average spring meroplankton community found in the Magellan region is characterised by highly variable abundances (Table 1) and an overwhelming amount of crustaceans, namely decapod and cirripede larvae, contributing 47 and 8% to overall abundance means, respectively (Table 1, Fig. 2A). Polychaete

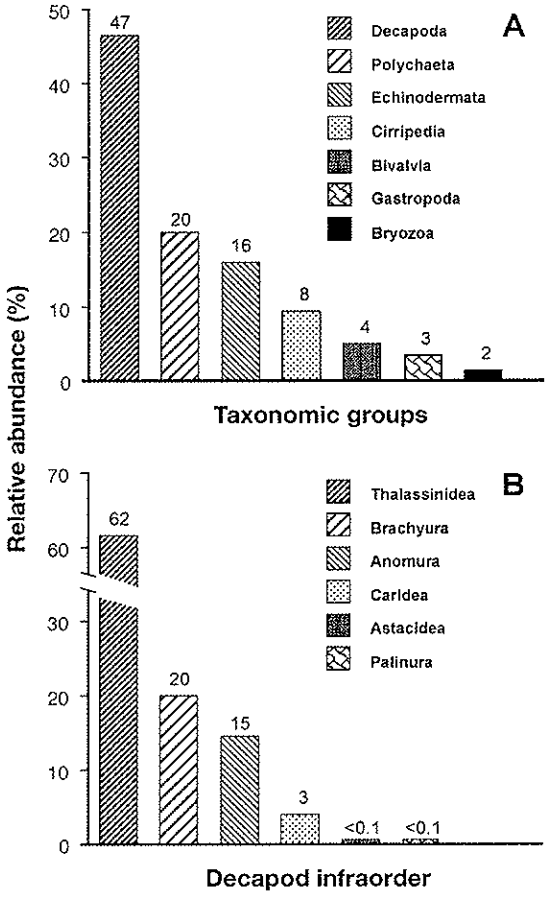

Fig. 2. Relative abundance of meroplankton fractions found in the channel and fjord system of the Magellan region in November 1994. Given on the basis of (A) major taxonomic groups and (B) decapod infraorder

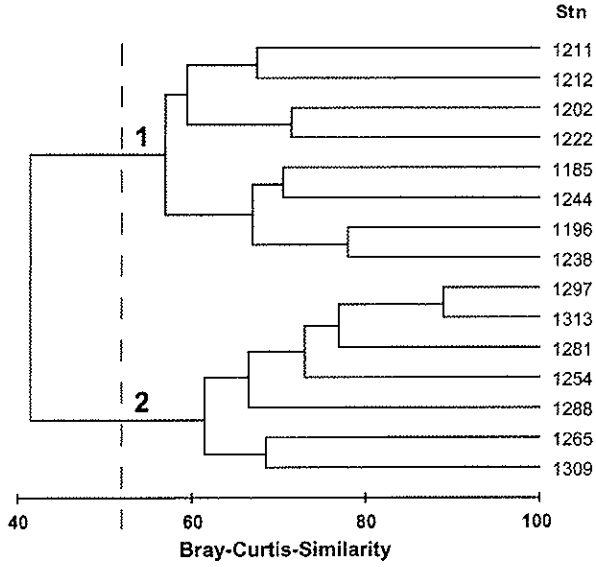

Fig. 3. Cluster dendrogramm (Bray-Curtis similarity) showing classification of meroplankton stations on the basis of abundance means

larvae ran second (20%) followed by echinoderms (16%); molluscs and bryozoans had much lower fractions (Fig. 2A). Within the decapod fraction, thalassinid larvae were found to be most abundant (62%), followed by brachyurans (20%) and anomurans (15%) (Fig. 2B). Caridean shrimp larvae, Astacidea and Palinura were of minor importance (Fig 2B). Also, in terms of species/morphotype richness, decapods were the dominant group within the meroplankton, with 2 thalassinid, 1 astacid, 1 palinurid, 5 brachyuran, 4 anomuran and 6 caridean species distinguished (the 2 pagurid species *Pagurus forceps* and *P. comptus* are combined as *Pagurus* spp., due to the lack of knowledge of the complete larval development in *P. forceps*; S. Thatje & G. Lovrich unpubl. data). Species determination of all other groups was complicated by the lack of adequate taxonomic keys, and therefore species richness must be considered as a minimum estimate on the basis of distinguished morphotypes: 3 bivalve, 2 gastropod, 2 to 4 ophiuroid, 1 echinoid, 1 cirripede and 1 bryozoan morphotypes were found. Polychaetes were more diverse, but remain to be further taxonomically identified. However, in relation to abundance, spionid larvae were the most dominant taxon (>60%).

Cluster analyses of the meroplankton composition revealed 2 groupings at the 55% similarity level (Fig. 3). Group 1 comprises shallow-water stations with depths varying from 30 to 100 m (Table 1) at the eastern entrance of the Beagle Channel, including Stn 1202 off Isla Wollaston (Fig. 1, Stns 1185 to 1244). Group 2 com-

bines 7 deep-water stations on a transect from the Straits of Magellan south to the Beagle Channel, with depths varying from 250 to 400 m (Figs. 1 & 3, Table 1).

Shallow-water stations are overwhelmingly dominated by decapods (91%, Fig. 4C) of which thalassinid larvae are most important (68%, Fig. 4D), followed by brachyuran (16%) and anomuran larvae (15%). Polychaete, cirripede and gastropod larvae contribute with only 4, 3 and 2%, respectively (Fig. 4C). Deep-water stations showed a more heterogeneous meroplankton composition (Fig. 4A), with polychaetes contributing 33%, followed by echinoderms (27%), cirripedes (13%), decapods (12%), bivalves (7%), gastropods (4%) and bryozoans (4%). The generally less important decapod fraction is dominated by brachyuran crab larvae (61%), carideans (24%) and anomurans (12%, Fig. 4B).

The meroplankton composition on a transect of deep-water station from the Straits of Magellan southward to the Beagle Channel differed totally from that of shallow-water stations (Figs. 1 & 5). Here, polychaetes and echinoderms were the dominant taxa. Only Stns 1281 and 1254 showed a percentage of cirripede larvae untypical of deep-water stations, although they were very similar in their taxonomic composition, despite the lack of echinoderms, to Stn 1222 from the eastern entrance of the Beagle Channel. The numerical dominance of decapod larvae at the shallow-water stations is correlated with a mass-occurrence of thalassinid larvae at almost all stations (Fig. 5A,B). At shallow-water stations, in contrast to deep-water stations, anomuran larvae were proportionally dominant over brachyuran larvae (Fig. 5B).

Vertical distribution of larvae

At some stations with a strong thermocline, a concentration of meroplanktonic larvae was found (Stns 1254, 1281, 1288, Fig. 6). This holds true especially for cirripede nauplii and echinoderm larvae (Fig. 6), which were concentrated in the thermocline.

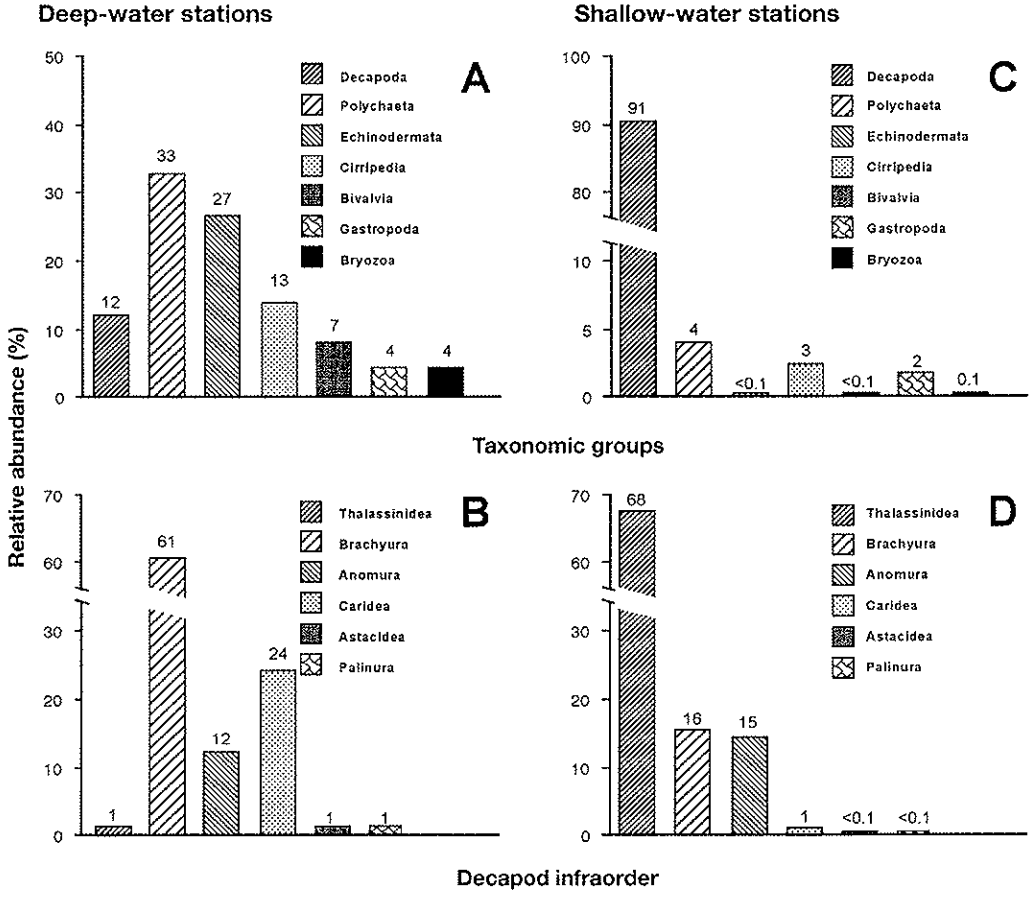

Fig. 4. Relative abundance of meroplankton fractions found in the channel and fjord system of the Magellan region in November 1994. Comparison of deep-water station means (A,B) with that of shallow-water stations. Given on the basis of (A,C) major taxonomic groups, (B,D) decapod infraorder

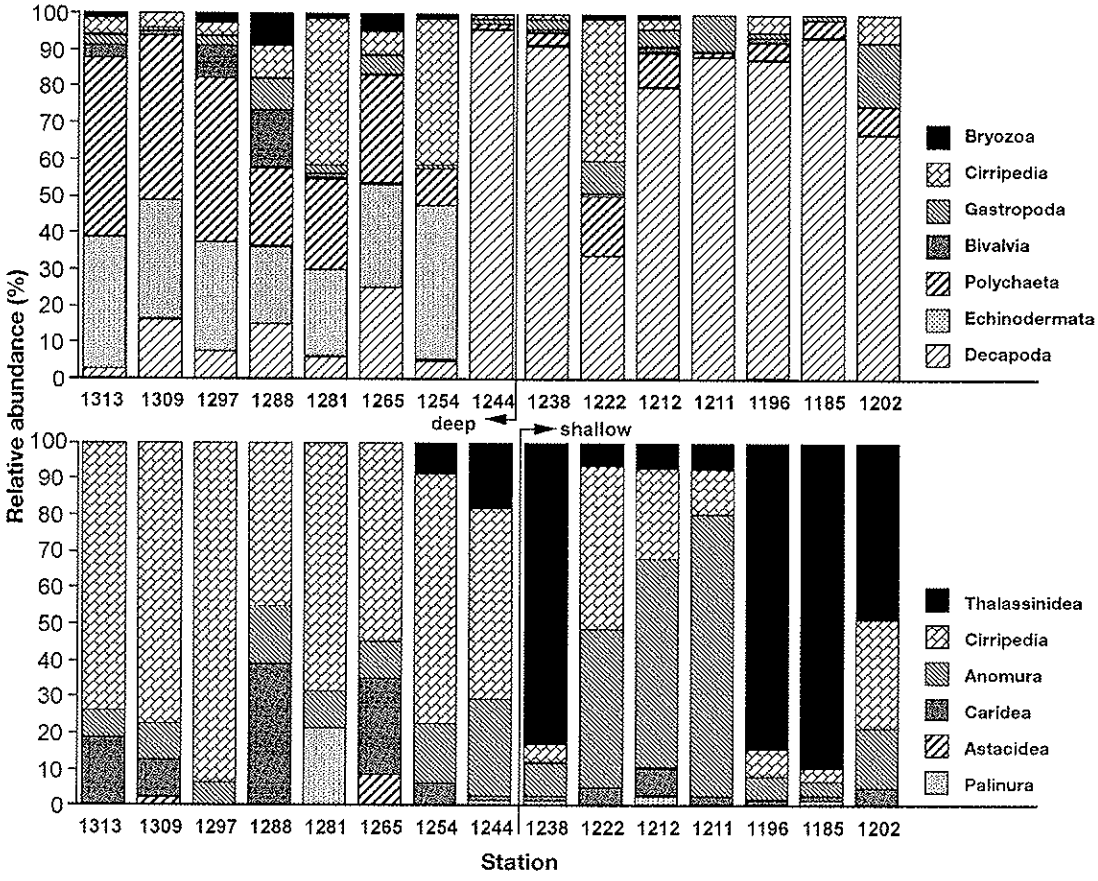

Fig. 5. Relative abundance of meroplankton fractions found at each station sampled in the Magellan region in November 1994. Given on the basis of (A) major taxonomic groups, (B) decapod infraorder

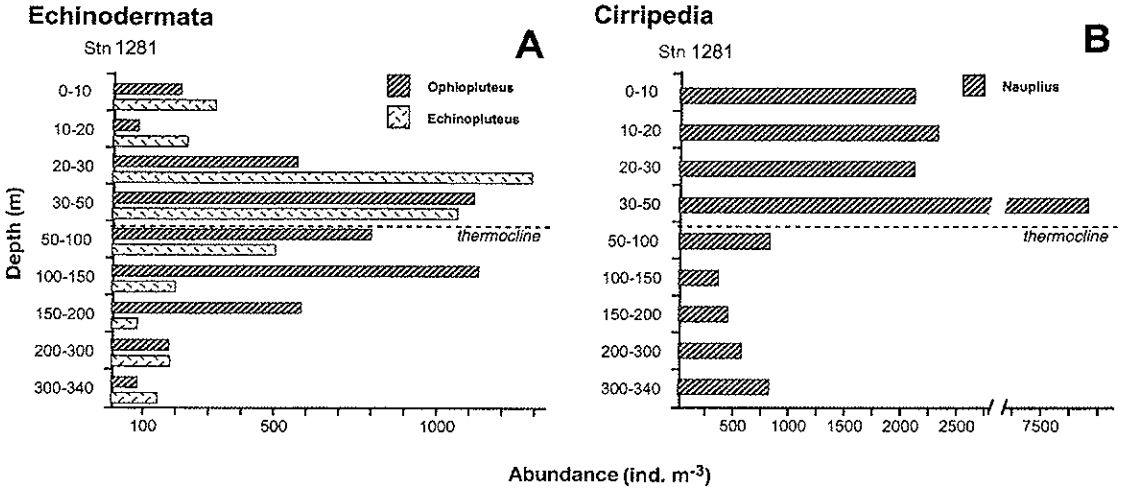

Fig. 6. Vertical distribution of echinoderm and cirripede larvae at Stn 1281. Dotted line = thermocline (at 70 to 80 m water depth, see Antezana et al. 1996)

Decapod larvae presented a distinct distribution: thalassinid larvae (*Notiax* sp.) were found in conspicuous numbers demersally just above the seafloor (Fig. 7), especially in an advanced stage of larval development. The brachyuran *Eurypodius latreillei* and the caridean *Austropandalus grayi* were found in high abundances at Stn 1288, which presented a strong thermocline (Fig. 7, see also Antezana et al. 1996). All larval stages of these 2 species were found below the thermocline, but only in the case of *A. grayi* did their distribution extend to the seafloor (Fig. 7). A very similar pattern to *E. latreillei* was found for larvae of *Munida* spp. and *Notiax* spp. (Fig. 7) at Stn 1238. Data on temperature and salinity are not available from this station, and therefore it is not known whether a well-developed thermocline was present there.

Developmental modes in decapod larvae

Three basic criteria of (1) morphogenesis, (2) mode of larval nutrition and (3) site of larval development were applied to characterise developmental modes in decapod larvae (cf. 'Materials and methods'). Independent of decapod infraorder, 3 basic larval developmental patterns were detected for the Magellan and south-western Atlantic decapod fauna (Table 2).

- Extended, planktotrophic development of planktonic larvae
- Abbreviated, planktotrophic development of planktonic larvae
- Abbreviated, lecithotrophic development of demersally living larvae.

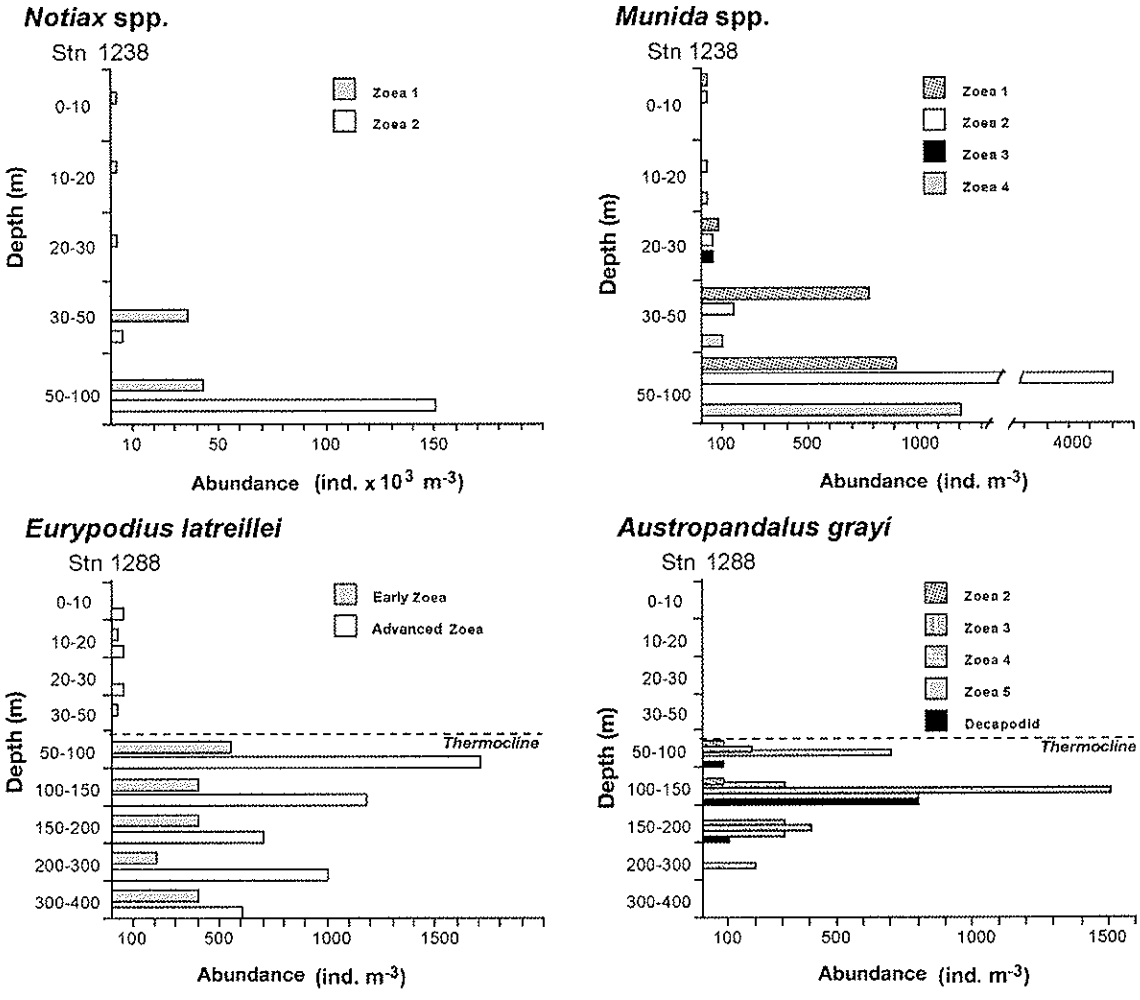

Fig. 7. Vertical distribution of selected decapod taxa from different sampling stations; *Notiax* sp. (Stn 1238), *Munida* spp. (Stn 1238), *Eurypodius latreillei* (Stn 1288), *Austropandalus grayi* (Stn 1288). Dotted line = thermocline (at 80 to 90 m water depth, see Antezana et al. 1996)

Table 2. Selected decapod taxa from the Magellan region and the southwestern Atlantic Ocean with partially or completely known mode of larval development. Biogeographical information was obtained from Gorny (1999). (?) Uncertain information

Species/Group	Duration		Nutrition		Habitat		Source
	Extend-ed	Abbre-viated	Plankto-trophic	Lecitho-trophic	Plank-tonic	Demer-sal	
Caridea							
Campylonotus vagans Bate, 1888		x	x		x		28, 30
Campylonotus semistriatus Bate, 1888		x	x		x		28
Chorismus antarcticus (Pfeffer, 1887)		x	x		x		6, 19
Chorismus tuberculatus Bate, 1888		x	x		x		26
Betaeus truncatus Dana, 1852	?		x		x		1, 29
Eualus dozei (A. Milne Edwards, 1891)	?						1
Nauticaris magellanica A. Milne Edwards, 1891		x	x		x		1, 27, 33, 34
Austropandalus grayi (Cunningham, 1871)	x		x		x		25
Palinura							
Stereomastis (*suhmi* Bate, 1878, ?)						x	21
Anomura							
Munida subrugosa Henderson, 1847	x		x		x		17, 22, 32, 35, 36
Munida gregaria (Fabricius, 1793)	x		x		x		17, 32, 35, 36
Lithodes santolla (Molina, 1782)		x		x		x	7, 9, 16, 18, 19
Paralomis granulosa (Jaquinot, 1847)		x		x		x	7, 8, 10, 16, 20
Pagurus comptus White, 1847	x		x		x		17, 23, 24, 31
Pagurus forceps H. Milne Edwards, 1836	x		x		x		17, 23, 24, 31
Parapagurus (*dimorphus* Smith, ?)						x	3, 21
Brachyura							
Eurypodius latreillei Guérin, 1828		x	x		x		2, 4, 11, 17
Libidoclaea granaria (H. Mil. Edw. & Lucas, 1842)	x		x		x		4, 12, 17
Halicarcinus planatus (Fabricius, 1775)	x		x		x		5, 17
Peltarion spinosulum (White, 1843)	x		x		x		14, 17
Pinnixia sp.	?		x		x		13, 17
Cancer edwardsi Bell, 1835	x		x		x		15
Astacidea							
Thymops birsteini (Zarenkov & Semenov, 1972)						?	21
Thalassinidea							
Notiax sp. (?)						x	21

Sources

(1) Albornoz & Wehrtmann (1997)
(2) Bacardit (1985b)
(3) Bacardit (1985a)
(4) Bacardit & Vera (1986)
(5) Boschi et al. (1969)
(6) Bruns (1992)
(7) Calcagno et al. (2003a)
(8) Calcagno et al. (2003b)
(9) Campodonico (1971)
(10) Campodonico & Guzman (1972)
(11) Campodonico & Guzman (1981)
(12) Fagetti (1969)
(13) Gutierrez-Martinez (1971)
(14) Iorio (1983)
(15) Quintana (1983)
(16) Kattner et al. (2003)
(17) Lovrich (1999)
(18) Lovrich et al. (2003)
(19) McLaughlin et al. (2001)
(20) McLaughlin et al. (2003)
(21) Present study
(22) Roberts (1973)
(23) Scelzo & Boschi (1969)
(24) Scelzo (1976)
(25) Thatje & Bacardit (2000a)
(26) Thatje & Bacardit (2000b)
(27) Thatje & Bacardit (2000c)
(28) Thatje et al. (2001)
(29) Thatje & Bacardit (2001)
(30) Thatje & Lovrich (2003)
(31) Thatje & Lovrich (unpubl.)
(32) Vera & Bacardit (1986)
(33) Wehrtmann & Albornoz (1998)
(34) Wehrtmann & Kattner (1998)
(35) Williams (1973)
(36) Williams (1980)

Brachyuran crabs seem to follow a general pattern of extended larval development, whereas caridean shrimp genera (*Chorismus*, *Campylonotus*, Table 2), which also have Antarctic representatives, follow an abbreviated larval development. Complete endotrophy in abbreviated larval development has so far only been recorded in lithodid crabs from the study area (Table 2).

DISCUSSION

Sampling method and identification of decapod larvae

Among several key ecological problems in high latitude marine larval biology is the general lack of early life history studies in marine invertebrates (but see

Pearse et al. 1991). This deficiency affects many aspects of ecological work and the development of ecological concepts, and only allows for broad generalisations as to larval developmental modes in the present study (Table 2). Sampling of meroplankton communities with a plankton net of 300 µm mesh size underestimated the true amount of invertebrate larvae. This should have affected meroplankton composition in particular, and especially smaller larval types, such as molluscs and echinderms, should be underrepresented. This should reduce the real decapod larval dominance to some extent. However, invertebrate larvae tend to be larger in cold temperate and polar regions (Thorson 1936, Mileikowsky 1971, Pearse et al. 1991), and this holds especially true for decapod larvae (Thatje & Bacardit 2000b,c, Thatje et al. 2001). The smallest decapod larvae known from the Beagle Channel is that of *Betaeus truncatus* (the Zoea I instar has an average total length of about 3.5 mm, see Thatje & Bacardit 2001), which was found in low abundance in our samples, and this species is generally known to occur in minor abundances within the benthic community (Pérez-Barros et al. in press).

All decapods which spend the greater part of their larval development in the plankton were considered planktotrophic, assuming that active feeding is necessary at least during part of the larval development, although development might be temporarily food independent, relying on high initial/maternal energy sources (for a review see Anger 2001). Since endotrophic larval development in benthic decapods tends to avoid pelagic phases (Anger et al. 2003, Lovrich et al. 2003) and complete lecithotrophic larval development is scarcely reported in marine carideans, we believe our generalisation in larval developmental modes to be a useful tool in describing decapod reproductive patterns. The definition of 'abbreviated' larval development in reptants is easy to apply, since most representatives (especially brachyuran crabs) usually develop through 4 to 6 zoeal stages and 1 megalopa stage (Williamson 1982, Anger 2001). A great variation in larval developmental pathways and larval instars has been described for caridean shrimps. We considered caridean larval developments as abbreviated when passing through 4 or less zoeal stages only, i.e. as in the genera *Campylonotus* (Thatje et al. in press) and *Chorismus* (Bruns 1992, Thatje & Bacardit 2000b). However, it has to be considered that this is a rather arbitrary definition of abbreviated development in carideans, which is only based on the number of instars, but does not take larval developmental times into account. The larval development of *Nauticaris magellanica* was also considered abbreviated (Table 2), as it was found to be reduced with increasing latitude (5 to 6 zoeal stages found in the present study area compared with 9 to 11 stages in central southern Chile, Wehrtmann & Albornoz 1998, Thatje & Bacardit 2000c).

Occurrence and distribution of invertebrate larvae

The difference in faunal composition between deep- and shallow-water stations (cf. Fig. 5) is due to the dominance of decapod crustaceans in the semi-enclosed hydrographic environment of the Beagle Channel, which is known for its richness in decapods (Gorny 1999, Pérez-Barros et al. unpubl.). Species richness in Subantarctic meroplankton is low and dominated in terms of abundance and diversity by decapod crustaceans with clear seasonal reproduction mainly taking place in spring (Lovrich 1999). It is not certain whether the high proportion of thalassinid larvae found in the Beagle Channel is due to the local distribution of the few species of this infraorder known from the area (see Thatje 2000, Thatje & Gerdes 2000), or to a direct coupling with larval release at the Beagle Channel stations. However, thalassinid shrimps depend on muddy to sandy sediments, which are abundant in the Beagle Channel, but coarser and more heterogeneous sediments are known on the station transect northward to the Straits of Magellan (Fig. 1) (Brambati et al. 1991). Decapod larval development seems to take place mainly in the midwater masses below the thermocline (if developed), where plankton particles are enriched, and consequently food availability is high. However, further studies are needed to define whether larvae show a vertical migration tendency, which may affect this distribution pattern. Decapod species that develop through demersally occurring larvae only, which are mostly of abbreviated and food-independent development as in lithodid crabs (McLaughlin et al. 2001, Calcagno et al. 2003a, Kattner et al. 2003), are rarely found in plankton hauls (Lovrich 1999).

The phylogenetic constraint of being tied to planktotrophic larval developments

The reason why caridean shrimps are successful in Antarctic waters has been assigned to their ability to down-regulate high Mg^{2+} concentrations in the haemolymph (Frederich et al. 2001); a mechanism which functions insufficiently in reptants. Despite this physiological ability to maintain activity levels in the cold (which remains scarcely studied in larvae), carideans show a great flexibility in larval developmental pathways at lower latitudes. This flexibility increases with the number of larval instars, and enhances larval dis-

persal and survival (Anger 2001). The requirements for exogenous energy from food allowing for developmental flexibility and extended modes of larval development should be high, as metabolic costs for additional moults as well as energy losses with cast exuviae imply a high degree of dependence on plankton productivity (Wehrtmann 1991, Anger 2001). Nevertheless, the flexibility in larval developmental pathways also allowed carideans to evolve energy saving strategies when low temperatures and limited food availability selected for abbreviated and partially endotrophic modes of larval development. This has been hypothesised as a latitudinal pattern in reproductive traits in carideans such as an increase, from the equator towards the poles, in egg size, in initial energy reserves of eggs and larvae, and in larval size, coinciding with a reduction in fecundity and in the age at first maturity (Arntz et al. 1992, Thatje et al. in press a,b). The need for such energy saving strategies under conditions of low temperatures and a seasonally limited primary production in high latitudes has suppressed the extent and flexibility of developmental pathways in caridean larvae. For instance, strongly abbreviated larval developments passing invariably through only 2 or 4 larval instars in the sub- and high Antarctic genera *Campylonotus* and *Chorismus*, respectively (Table 2) (Bruns 1992, Thatje & Bacardit 2000b, Thatje et al. in press a), combined with high larval resistance to starvation, especially in the Zoea 1 instar (Thatje et al. in press a,b), allow for an enhanced synchronisation with short and pulsed periods of primary production, and simultaneously reduce the degree of larval dependence on planktonic food sources (Clarke 1988, Anger et al. 2003). Similar early life history adaptations are known also from the Antarctic crangonid *Notocrangon antarcticus* (Bruns 1992). In the high Antarctic Weddell Sea, carideans are able to spawn only every second year (Arntz et al. 1992, Gorny et al. 1992, Gorny & George 1997), suggesting a lack of sufficient energy supply to female reproduction, due to short periods of primary production during summer, which may be insufficient for the level of somatic growth allowing for an annual reproductive cycle (Clarke 1982). In polar environments, the mismatch between energy availability and high costs for female energy investment into large embryos might thus have selected against complete lecithotrophy in caridean larval development. On the other hand, complete endotrophic larval development of pelagic larvae is rare in marine caridean shrimps (although frequently recorded in shrimps from limnic systems, especially Palaemonidae, cf. Magalhães 1988, Odinetz Collart & Magalhães 1994), which may indicate a phylogenetic constraint for the evolution of lecithotrophic developments in the sea. One known exception, which should be mentioned here, is the Subarctic *Sclerocrangon boreas*, which has a direct and abbreviated (lecithotrophic) development of benthic larvae, including a high degree of parental care (Makarov 1968, Miglavs 1992).

In general, brachyuran crabs have an extended planktotrophic mode of larval development. Cases of an abbreviated development or flexibility in the number of instars have usually been observed under conditions of physiological stress (Anger 2001) and as special adaptations to breeding in land-locked limnic or terrestrial habitats (Montú et al. 1990, Anger & Schuh 1992, Anger 2001). An abbreviated larval development in some endemic terrestrial grapsoid crabs from Jamaica, for instance, has been shown to be a recent evolutionary adaptation to semi-terrestrial or terrestrial life (Schubart et al. 1998), which evolved only about 4 million years ago (for a discussion see Anger 2001). Resistance of brachyuran larvae to starvation is generally low, and examples of larval exposure to low temperatures have indicated that the use of energy sources is hampered by metabolic disturbance below critical temperatures (Anger et al. 1981, Pörtner 2002). The inability of most reptant decapods to suppress the number of larval stages should therefore have selected against their occurrence in high latitudes when the Antarctic region began to become cooler (Clarke 1990). However, one family of anomuran crabs, the lithodid crabs, which in evolutionary terms evolved quite recently, developed complete endotrophic larval development of demersal larvae. They evolved from hermit crab ancestors (Cunningham et al. 1992, this phylogenetic relation is the subject of recent controversial discussion, see also McLaughlin & Lemaitre 2000), and were recorded for the first time between 13 to 25 million years ago, when other much older brachyuran and anomuran taxa (hermit crabs evolved more than 150 million years ago, Cunningham et al. 1992 and references therein) were already extinct in high southern latitudes due to Antarctic cooling (Zinsmeister & Feldmann 1984, Feldmann & Tshudy 1989). Lithodid crabs from the Magellan region (*Paralomis granulosa*, *Lithodes santolla*) developed special adaptations in life history, such as prolonged brooding of egg masses and, most importantly, complete lecithotrophy in larval development, which allowed for adaptation to ecological and physiological constraints in high latitudes (Frederich et al. 2001, Anger et al. 2003, Lovrich et al. 2003, Thatje et al. 2003). This evolutionarily young taxon of anomuran crabs, which is represented by several species in high latitudes of both hemispheres and also appears to be a common deep-sea representative (Anger et al. 2003 and references therein), is obviously about to release itself from the apparent phylogenetic constraints that have prevented reptants from conquering the polar marine realm as a

life habitat (Macpherson 1988, Klages et al. 1995, Arana & Retamal 2000). We suggest a similar recent evolutionary trait to be responsible for abbreviated larval developments in spider crabs (Majidae), which are already present in both the Subarctic (e.g. *Hyas araneus*, Dyer 1985) and the Subantarctic (*Eurypodius latreillei*). *Eurypodius latreillei* Guerin, which at present is the southernmost known spider crab in the southern hemisphere, was recently confirmed to occur in waters off South Georgia (Romero et al. 2003). The Majidae are suggested as further possible recolonisers of the Polar marine realm.

Acknowledgements. We would like to thank the crew of the German RV 'Victor Hensen' for assistance at sea. Tanja Joschko and Mario Hubo helped in separating the meroplankton fraction. Claudio Richter (ZMT, Bremen) kindly provided the plankton samples. The authors would like to thank Klaus Anger and Gustavo Lovrich as well as Ingo Wehrtmann and 3 anonymous reviewers for critically commenting on the manuscript. Thanks are due to Ruth Alheit for her revision of the English.

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: April 23, 2003; Accepted: July 15, 2003
Proofs received from author(s): September 4, 2003

ELSEVIER

Journal of Experimental Marine Biology and Ecology
288 (2003) 65–79

Journal of EXPERIMENTAL MARINE BIOLOGY AND ECOLOGY

www.elsevier.com/locate/jembe

Changes in biomass and chemical composition during lecithotrophic larval development of the southern king crab, *Lithodes santolla* (Molina)

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Received 13 September 2002; received in revised form 8 November 2002; accepted 5 December 2002

Abstract

Changes in biomass and elemental composition (dry mass, *W*; carbon, C; nitrogen, N; hydrogen, H) were studied in the laboratory during complete larval and early juvenile development of the southern king crab, *Lithodes santolla* (Molina), formerly known as *Lithodes antarcticus* (Jacquinot). At 6 ± 0.5 °C, total larval development from hatching to metamorphosis lasted about 10 weeks, comprising three demersal zoeal stages and a benthic megalopa, with mean stage durations of 4, 7, 11 and 47 days, respectively. No differences in development duration or mortality were observed in larvae either fed with *Artemia* sp. nauplii or unfed, indicating that all larval stages of *L. santolla* are lecithotrophic. First feeding and growth were consistently observed immediately after metamorphosis to the first juvenile crab stage. Regardless of the presence or absence of food, *W*, C, N and H decreased throughout larval development. Also the C:N mass ratio decreased significantly, from 7.7 at hatching to 4.1 at metamorphosis, indicating that a large initial lipid store remaining from the egg yolk was gradually utilized as an internal energy source, while proteins played a minor role as a metabolic substrate. In total, 56–58% of the initial quantities of C and H present at hatching, and 20% of N were lost during nonfeeding larval development to metamorphosis. Nine to ten percent of the initially present C, N and H were lost with larval exuviae, half of these losses occurring in the three zoeal stages combined and another half in the megalopa stage alone. Metabolic biomass

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0022-0981/03/$ - see front matter
doi:10.1016/S0022-0981(02)00596-8

degradation accounted for losses of about 47–50% in C and H but for only 10% in N. Hence, most of the losses in C and H reflected metabolic energy consumption (primarily lipid degradation), while about half of the losses in N and two thirds of those in *W* were due to larval exuviation. Complete independence from food throughout larval development is based on an enhanced maternal energy investment per offspring and on energy-saving mechanisms such as low larval locomotory activity and low exuvial losses. These traits are interpreted as bioenergetic adaptations to food-limited conditions in Subantarctic regions, where a pronounced seasonality of day length limits the period of primary production, while low temperatures enforce a long duration of pelagic development.

Keywords: Cold adaptation; Crustacea; Larval development; Lecithotrophy; Lithodidae; Reproductive strategies

1. Introduction

Lithodid crabs, in general, represent an important fishery target in cold and temperate regions of both hemispheres, and, as a consequence of their commercial value, an extensive literature is available on their growth, feeding, taxonomy and fisheries management (for references, see Dawson, 1989; Lovrich, 1997). The southern king crab, *Lithodes santolla* (Molina), formerly known as *Lithodes antarcticus* (Jacquinot), is a typical example, constituting an important part of the local artisanal trap fishery in the Argentine and Chilean parts of Tierra del Fuego, the Strait of Magellan, and in adjacent channels and fjords (Campodonico, 1971; Lovrich, 1997).

In contrast to the biology of adult lithodids, that of the early life-cycle stages has remained scarcely known (Nakanishi, 1985; Anger, 1996). Several studies have paid attention to the larval morphology, development and ecology of *L. santolla* (Campodonico, 1971; Vinuesa et al., 1985; Comoglio and Vinuesa, 1991; Amin et al., 1998; Lovrich and Vinuesa, 1996, 1999; Lovrich, 1999; McLaughlin et al., 2001), while no information has been available on changes in biomass and chemical composition during larval development. In a previous investigation on a congener, the northern king crab (*Lithodes maja*), decreasing biomass values in both fed and unfed larvae indicated a completely endotrophic mode of development (Anger, 1996). Based on similarities in several larval traits (e.g. three zoeal stages and big yolky larvae), the author suggested that the southern king crab may show the same mode of development, tentatively interpreting their lecithotrophy as an adaptation to planktonic food limitation in high latitudes. In the present study, we analysed the role of external food for larval and early juvenile development in *L. santolla*, comparing changes in dry mass and in the contents of organically bound elements (carbon, nitrogen, hydrogen) of fed and unfed larvae.

2. Materials and methods

2.1. Capture and maintenance of ovigerous females

Ovigerous females of *L. santolla* were caught in April 2000 from ca. 15 to 30 m depths in the Beagle Channel (54°53.8′ S, 68°17.0′ W) using commercial fishery traps. The crabs

were kept in aquaria at 6 ± 0.5 °C in the local institute "Centro Austral de Investigaciones Científicas" (CADIC) in Ushuaia, Argentina. In May, they were transported on board the German scientific research vessel PFS Polarstern to Bremerhaven and subsequently to the marine biological laboratory Helgoland, Germany. During this transport, which took about 1 month, water was changed three times a week and food (squid) was given twice a week. The maintenance of females and, later, the rearing of larvae took place under constant conditions of temperature (6 ± 0.5 °C) and salinity (32 ‰), with an artificial 12:12-h light/dark cycle. The ovigerous females were kept individually in flow-through tanks with at least 10 l seawater.

2.2. Rearing of larvae and juveniles

Freshly hatched larvae were collected in filters receiving the overflow from the aquaria. Since most larvae hatched at night, samples were taken every morning. Filters were cleaned every evening to ensure that larval age did not vary more than by 12 h.

Actively moving larvae were randomly selected and kept in individual bowls with about 100 ml seawater. In one treatment, the larvae were reared from hatching through to metamorphosis in complete absence of food, while in a second treatment, the larvae were fed with freshly hatched *Artemia* nauplii (Argent Chemical Laboratories, USA). In this experiment, we sampled megalopae and juvenile crabs only once each, at the beginning of their moulting cycles.

In another experiment, larvae from the same female were reared without food until they reached the megalopa stage. Subsequently, changes in biomass and chemical composition were studied with a higher temporal resolution throughout the megalopa and crab I stages, comparing again a fed and an unfed group in the megalopa; juveniles were always fed.

The larvae were checked daily for deaths or moults, and shed exuviae were sampled for later analyses of lost biomass (see below). Water was changed every 2 days and, where appropriate, food was supplied.

The larvae passed invariably through three zoeal stages and one megalopa. The separation of the different stages was done on the basis of an appearing exuvia and morphological changes in the larvae (Campodonico, 1971; McLaughlin et al., 2001). The zoeal II differs from the first stage in the presence of small but conspicuous pleopod buds. The zoea III shows developed but still nonfunctional pleopods.

When larvae reached the benthic megalopa, a piece of nylon mesh was placed in each bowl as an artificial substrate, which facilitated the settlement and metamorphosis of the megalopa.

2.3. Sampling for elemental and biochemical analyses

All larvae sampled from the first experiment for elemental and biochemical analyses originated from the same female. Larvae from a second female were used to study biomass changes in the megalopa and first juvenile. Samples for determinations of dry mass (W) and elemental composition (C, N, H; with $n = 5$ replicates each; one individual per replicate) were taken immediately after hatching and in variable intervals during later development (see Table 1). Exuviae were sampled from each larval stage in order to

Table 1
L. santolla. Changes in dry mass (*W*) and contents of carbon (C), nitrogen (N) and hydrogen (H) (all in % of *W*; $\bar{x} \pm$ S.D.) during larval development in presence or absence of food (*Artemia* sp.) and during growth of the first juvenile crab stage (always fed); age given in days (a) within each stage and (b) after hatching

Stage	Age		*W* (μg/individual)				C (% of *W*)				N (% of *W*)				H (% of *W*)			
	(a)	(b)	With *Artemia*		Without *Artemia*		With *Artemia*		Without *Artemia*		With *Artemia*		Without *Artemia*		With *Artemia*		Without *Artemia*	
			$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.
Zoea I	0	0	1017	76	1017	76	54.5	0.7	54.5	0.7	7.1	0.2	7.1	0.2	8.2	0.1	8.2	0.1
	4	4	1002	13	957	69	55.3	0.4	55.1	0.6	7.4	0.1	7.4	0.1	8.5	0.1	8.4	0.1
Zoea II	0	5	920	61	958	62	54.0	0.7	54.7	1.1	7.2	0.2	7.2	0.2	8.1	0.1	8.4	0.2
Zoea III	0	11	930	34	882	94	51.7	0.9	51.7	1.0	7.5	0.2	7.7	0.3	8.0	0.2	8.0	0.1
Megalopa	0	22	821	44	768	70	50.7	0.5	50.5	0.7	8.2	0.3	8.0	0.3	7.8	0.1	7.5	0.1
	10	32	938	111	914	96	42.2	2.7	41.6	0.8	7.0	0.4	7.2	0.1	6.2	0.4	6.1	0.1
	20	42	869	113	883	90	37.7	0.6	38.8	1.3	6.8	0.2	7.3	0.3	5.5	0.1	5.6	0.2
	30	52	944	55	868	101	35.5	2.0	35.4	1.9	6.9	0.2	6.9	0.0	5.2	0.3	5.1	0.3
	40	62	765	40	747	60	35.3	0.8	36.8	1.2	7.9	0.3	8.3	0.3	5.0	0.2	5.2	0.2
Crab I	0	66	666	82	561	168	40.4	3.7	39.3	1.6	8.4	0.8	8.9	0.6	5.9	0.6	5.6	0.3
	2	68	801	176			36.1	9.6			7.1	1.6			5.0	1.4		
	5	71	1385	190			26.1	0.8			4.7	0.2			3.4	0.1		
	10	76	1722	116			24.9	0.6			4.3	0.2			3.2	0.1		
	15	81	1677	66			26.0	1.7			4.6	0.1			3.4	0.3		
	20	86	1794	98			27.4	0.5			4.9	0.1			3.5	0.1		
	25	91	2008	150			28.2	0.9			5.1	0.1			3.6	0.2		
	30	96	1826	336			27.3	2.1			5.0	0.4			3.5	0.3		
	35	101	1998	92			28.1	0.7			5.4	0.1			3.7	0.1		
	40	106	1732	201			27.8	1.5			5.5	0.5			3.6	0.2		
Crab II	0	107	1261	60			36.7	2.5			8.6	0.8			5.5	0.4		

quantify biomass losses during successive moults. Since a minimum of 0.2 μg dry mass is needed for each elemental analysis, 20 exuviae (originating from various females) per replicate sample were pooled.

Weight measurements were carried out to the nearest 0.1 μg with an autobalance (Mettler, UMT 2). Techniques and equipment used for obtaining C, N and H content of larvae and young crabs are described by Anger and Harms (1990): short rinsing in distilled water, blotting on fluff-free Kleenex paper for optical use, freezing at −18 °C, vacuum drying at $<10^{-2}$ mbar, weighing and combusting at 1020 °C in a Fison Carlo Erba 1108 Elemental Analyser.

2.4. Statistical treatments

For both treatments (with and without *Artemia* provided as an external food supply), changes in biomass parameters (*W*, C, N, H) were described and compared with linear regressions as functions of larval age (Sokal and Rohlf, 1995). The data were first log-transformed to achieve normality and homoscedasticity (tested with Kolmogorov–Smirnov and Bartlett's tests, respectively). Since biomass measurements for the developmental phases zoea–megalopa and megalopa–crab II were done with larvae obtained from the same female but hatched on different days, results and statistical analyses were carried out separately for each phase. Slope parameters of linear regressions obtained from treatments with and without feeding were compared an analysis of covariance (ANCOVA; Sokal and Rohlf, 1995). Where average values with error estimates are given in the text or in figures and tables, these represent arithmetic mean values ± one standard deviation (S.D.).

3. Results

3.1. Larval development

The zoea I took on average about 4, the zoea II 7, and the zoea III 10–11 days. Most of the larval development time was spent in the megalopa, lasting 42–50 days. The absence or presence of food did not influence development duration or survival, and corresponding results are reported elsewhere (Calcagno et al., submitted for publication a,b).

3.2. Dry mass, percentage C, N and H, and C:N ratio

Dry mass (*W*) decreased continuously from hatching to metamorphosis, regardless of food availability (Table 1; Figs. 1 and 2). Near the end of the megalopa stage (day 40 within this stage, 62 days after hatching), the average *W* of fed or unfed individuals amounted to about 73–75% of the initial value measured at hatching. The proportional losses of the elements C and H (predominantly bound in organic compounds) were, in general, higher than those of total *W* and, as a consequence, their percentage values of *W* decreased significantly throughout larval development, with or without food (Table 1). The C fraction decreased from initially 54% to about 36% of *W*, H from 8% to 5% of *W*.

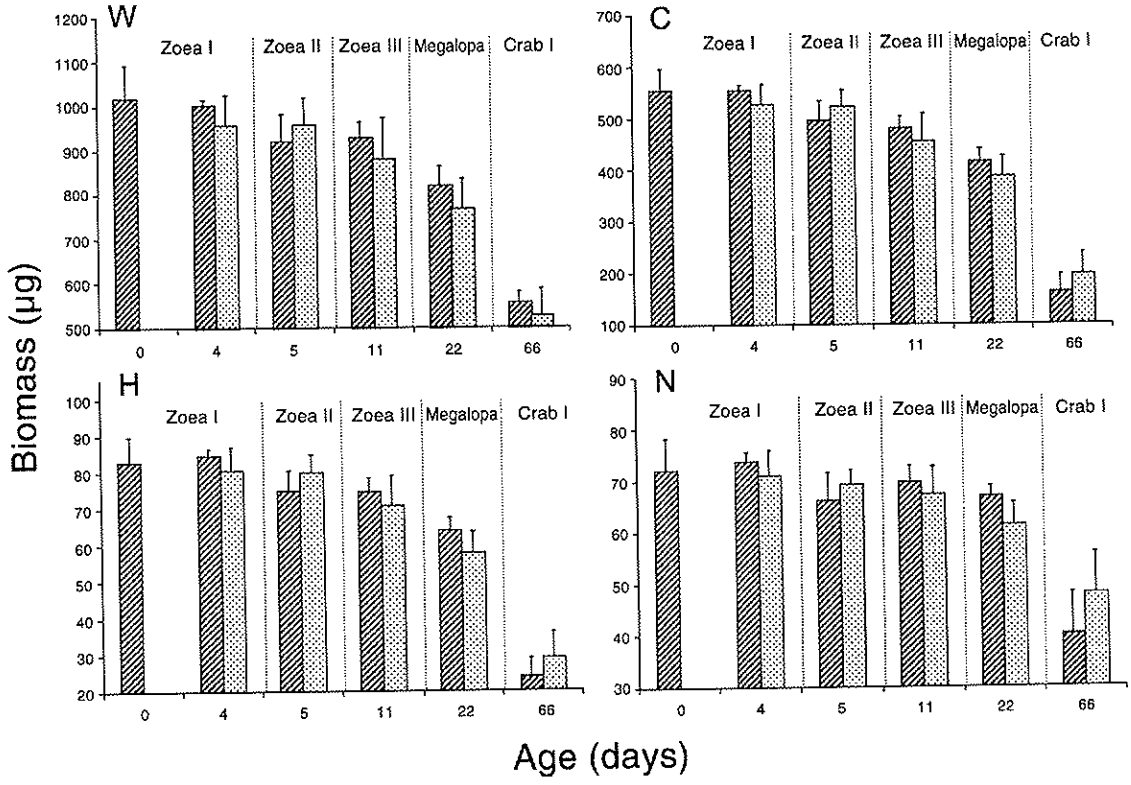

Fig. 1. *L. santolla*. Changes in dry mass (*W*) and contents of carbon (C), nitrogen (N) and hydrogen (H) (all in µg/individual; $\bar{x}$ + S.D.) during larval development from hatching to metamorphosis in the presence or absence of food (*Artemia* sp.). Striped bars = with *Artemia*; dotted bars = without *Artemia*. Sample size = 5.

In contrast to the percentage C and H values, the percentage N remained stable or increased slightly, indicating that this fraction changed in approximately the same proportions as total *W*. As a consequence of consistently higher losses in C as compared to N, the C:N mass ratio, which may be used as an indicator of the lipid/protein ratio, decreased significantly during larval development (Fig. 4). Very high C:N values were measured at hatching (7.7 ± 0.2), while significantly lower values occurred shortly before metamorphosis (4.4 ± 0.2 to 4.5 ± 0.1, in unfed and fed individuals, respectively). These patterns indicate a significant extent of lipid utilization throughout the course of larval development. Again, no influence of the presence or absence of food was apparent.

First feeding was consistently observed immediately after metamorphosis to the first juvenile crab stage, and this behavioural change was soon reflected in rapidly increasing dry mass values (Table 1; Fig. 3). However, *W* increased significantly only during the first ca. 25 days of the first juvenile moulting cycle; thereafter, it remained almost constant. Due to the loss of a comparably heavy exuvia (see below), the freshly moulted crab II instar showed a conspicuously lower dry mass than the late crab I (Fig. 3).

The percentage values of C, N and H within total *W* decreased rapidly during the initial period (postmoult) of the crab I moulting cycle (Table 1). Since the absolute values of

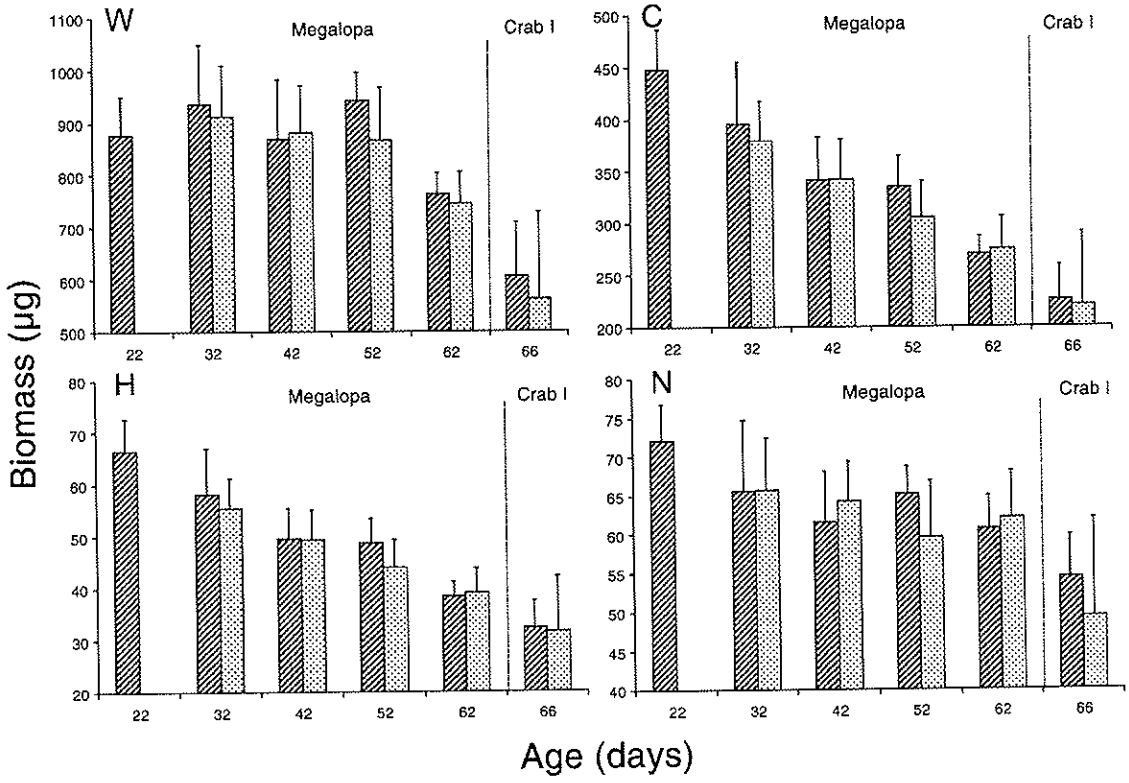

Fig. 2. *L. santolla*. Changes in dry mass (*W*) and contents of carbon (C), nitrogen (N) and hydrogen (H) (all in µg/individual; $\bar{x}$+S.D.) during megalopal development in the presence or absence of food (*Artemia* sp.). Striped bars = with *Artemia*; dotted bars = without *Artemia*. Sample size = 5.

these elements per individual increased (see below), decreasing percentage values indicate that total *W* (including the mineral fraction) increased initially faster than the organic fraction of biomass. Later during the moulting cycle, the percentage values of C, N and H increased slightly or remained constant (Table 1).

Also the average C:N mass ratio increased rapidly during the postmoult phase of the first juvenile stage, from an initial value of 4.8 ± 0.3 to a maximum of 5.9 ± 0.2 about 10 days after metamorphosis. This increase was followed by slightly decreasing values in premoult (Fig. 4). A much lower value (4.3 ± 0.1) was found in the freshly moulted crab II stage.

3.3. Organic biomass (C, N, H) per individual

The absolute contents of C, N and H (in µg/individual), which are considered as measures of chiefly organic biomass, changed during the time of larval and early juvenile development with similar patterns as total dry mass (*W*) (Figs. 1–3). The rates of change, however, in C and H were generally higher than in *W* and in N. When biomass values in a late megalopa (40 days) are compared with those measured immediately after hatching of the zoea I, differential degrees of utilization can be seen in the various measures biomass. While only about 26% of the initially present total *W*

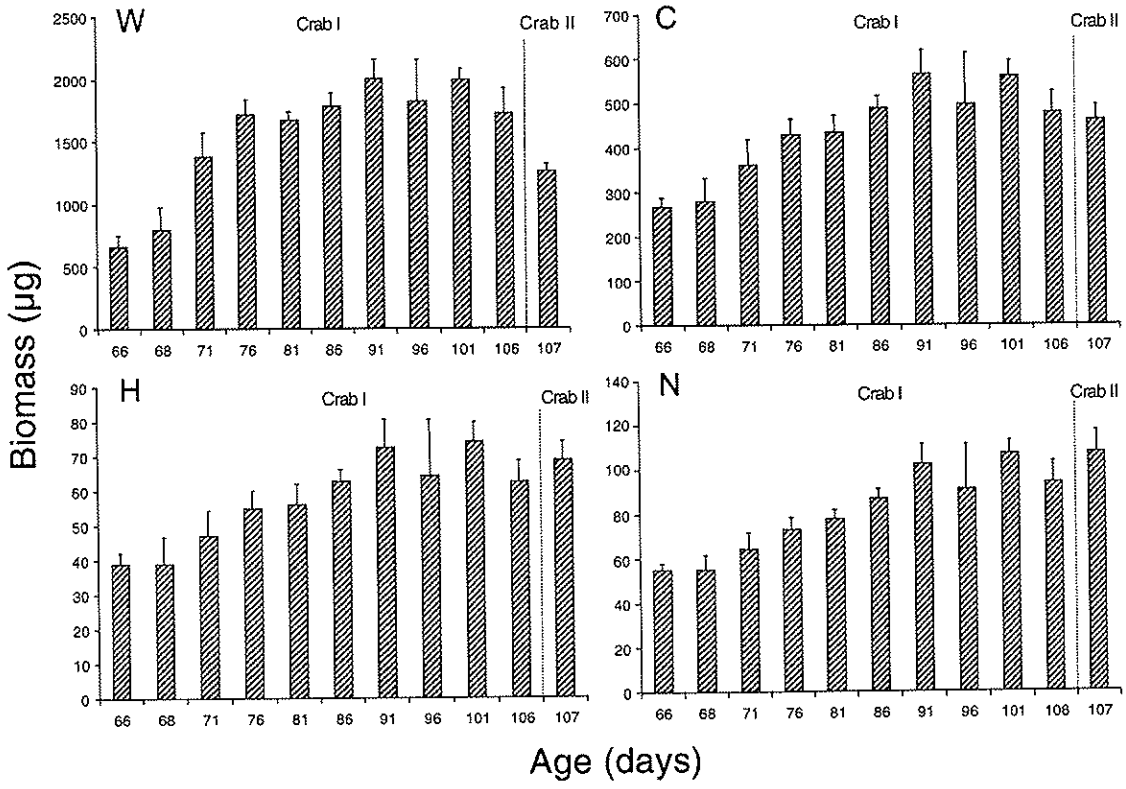

Fig. 3. *L. santolla*. Changes in dry mass (*W*) and contents of carbon (C), nitrogen (N) and hydrogen (H) (all in µg/individual; $\bar{x}$ + S.D.) during early juvenile development. Sample size = 5.

and 15% of N were lost during this developmental period (62 days from hatching), more than one half of the C and H fractions had disappeared concomitantly (51% and 54%, respectively). These losses include both the previous exuvial losses of the zoeal stages (but not yet that of the megalopa) and the metabolic degradation of organic substrates, which will be considered below.

Individual larval biomass decreased in a gradual manner. After logarithmic transformation of both the biomass and time data (the latter transformed to days + 1 in order to exclude zero values), these patterns of change in biomass could be described as linear functions of the time of development (Table 2). Statistical comparison of the slope parameters by means of an ANCOVA did not reveal significant differences in any measure of biomass of fed and unfed larvae. This corroborates again our inference that all larval stages of *L. santolla* are fully lecithotrophic and nonfeeding also in the presence of a planktonic food source.

From metamorphosis until day 25 of its moulting cycle, the first juvenile crab instar (always fed with *Artemia*) showed a continuous and significant increase in all measures of individual biomass (Fig. 3). During this period (postmoult and early intermoult), the biomass of a crab I increased on average about three times in total dry mass and to almost double the initial contents of C, N and H. The proportionally higher increase in *W* reflects the postmoult mineralization of the exoskeleton with inorganic constituents.

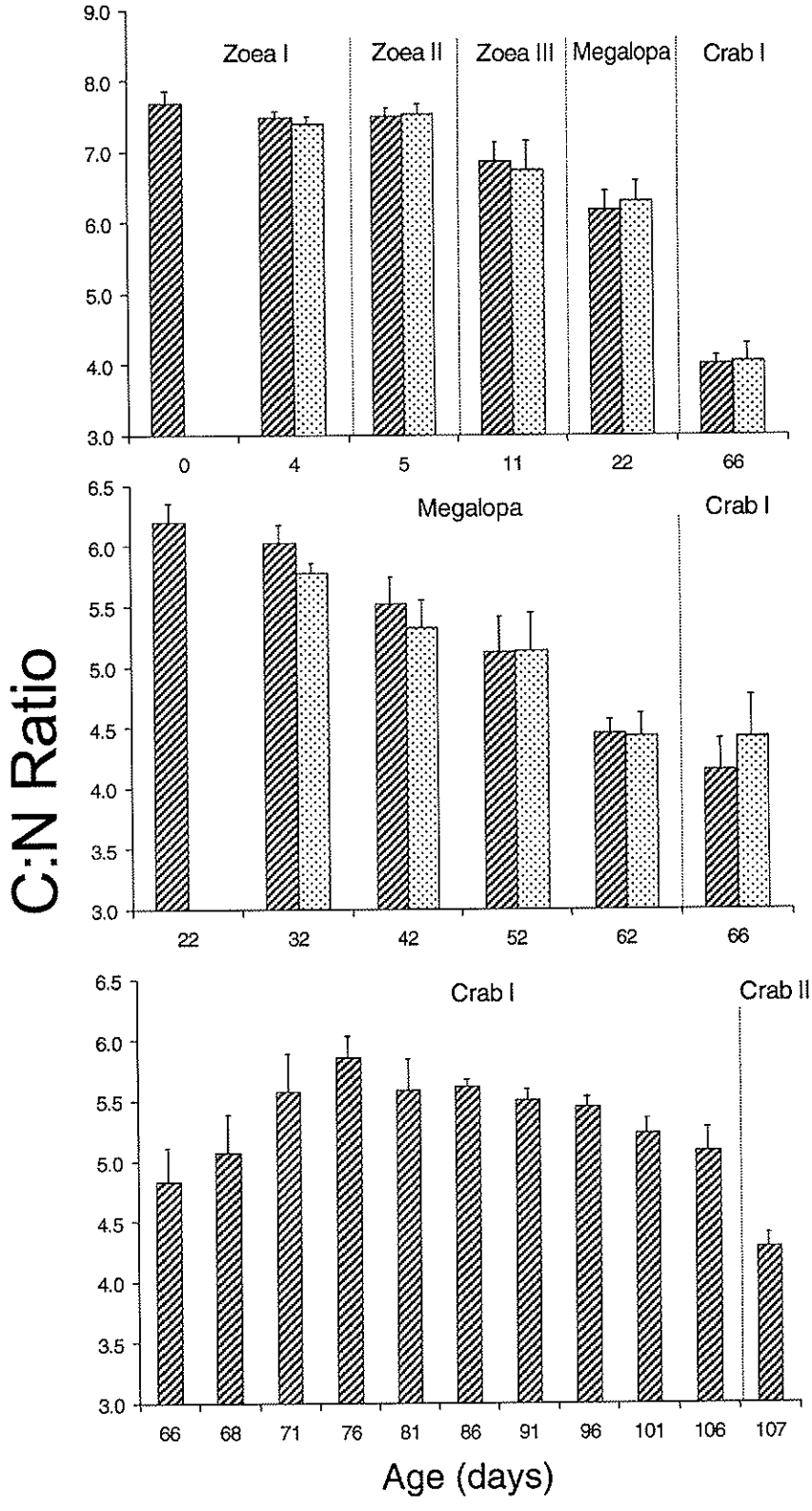

Fig. 4. *L. santolla*. Carbon/nitrogen (C:N) mass ratio during larval and early juvenile development. Striped bars = with *Artemia*; dotted bars = without *Artemia*. Sample size = 5.

Table 2
L. santolla. Parameters of linear regressions describing changes in dry mass (*W*), contents of carbon (C), nitrogen (N) and hydrogen (H) (all in μg/individual), and in the C:N mass ratio (all after logarithmic transformation) as functions of the time of development (transformation: log days+1) during two developmental periods (zoea I–III, megalopa) and in two treatments (with, without food, *Artemia* sp.)

Stage	Biomass parameter	With food			Without food			*P*
		Slope	Intercept	r^2	Slope	Intercept	r^2	
Zoea I–III	*W*	−0.004	3.005	0.606	−0.006	3.005	0.612	0.183
	C	−0.006	2.745	0.718	−0.007	2.747	0.710	0.187
	H	−0.005	1.923	0.649	−0.008	1.930	0.709	0.076
	N	−0.001	1.854	0.070	−0.003	1.860	0.420	0.074
	C:N	−0.004	0.891	0.891	−0.004	0.887	0.780	0.518
Megalopa	*W*	−0.003	3.045	0.305	−0.004	3.067	0.313	0.513
	C	−0.006	2.787	0.762	−0.006	2.788	0.644	0.787
	H	−0.006	1.968	0.771	−0.007	1.967	0.659	0.810
	N	−0.002	1.892	0.361	−0.003	1.918	0.319	0.364
	C:N	−0.004	0.895	0.889	−0.003	0.869	0.865	0.148

r^2: coefficient of determination; all slopes are significantly different from zero ($P<0.001$); the slopes of regressions obtained from the different treatments do not differ significantly from each other (ANCOVA: all $P>0.05$).

3.4. Exuvial losses

The biomass and elemental composition of larval exuviae is shown in Table 3. Due to technical difficulties obtaining a sufficiently high number of complete larval exuviae for analyses (these rapidly fall apart), there is a great deal of variability in our data, in particular in those of zoea II exuviae. Yet, the average values allow for comparing chemical traits of the exuviae with those of whole-body biomass and for estimating exuvial losses in relation to other (metabolic) losses of organic biomass.

Total dry mass and contents of C, N and H per exuvia were generally low and similar among the three zoeal stages, while significantly higher values were found in the

Table 3
L. santolla. Dry mass (*W*), contents of carbon (C), nitrogen (N) and hydrogen (H) (all in μg/individual and in % of *W*), and C:N mass ratio of the exuviae of all larval stages and the first juvenile crab; $\bar{x} \pm$ S.D.

Stage		*W*		C		N		H		C:N mass ratio	
		$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.	$\bar{x}$	± S.D.
Zoea I	μg/ind	37	5	8.5	0.6	1.7	0.1	1.2	0.1		
	% of *W*			23.7	2.2	4.6	0.4	3.4	0.2	5.2	0.1
Zoea II	μg/ind	32	10	5.9	0.6	0.8	0.2	0.8	0.1		
	% of *W*			19.0	3.7	2.7	1.3	2.7	0.8	8.1	3.5
Zoea III	μg/ind	33	3	7.3	0.4	1.3	0.0	1.1	0.1		
	% of *W*			22.2	1.0	3.9	0.3	3.4	0.1	5.7	0.2
Megalopa	μg/ind	182	15	26.9	1.8	3.5	0.2	3.8	0.3		
	% of *W*			14.8	0.6	1.9	0.2	2.1	0.1	7.8	0.4
Crab I	μg/ind	922	117	128.0	13.6	7.7	0.9	8.4	1.0		
	% of *W*			13.9	0.5	0.8	0.1	0.9	0.0	10.7	0.7

megalopa and crab I stages. The megalopa lost its exuvia at metamorphosis with similar or higher amounts of biomass than all zoeal stages combined, and the first juvenile crab lost more exuvial matter (especially *W* and C) than all larval stages (i.e. all zoeal stages and the megalopa) combined.

As a striking feature of the exuviae, the percentage C, N and H values (in % of *W*) were, in general, far below those of whole-body biomass, while the exuvial C:N mass ratio was mostly higher than in entire larval and early juvenile bodies (cf. Table 1). When exuviae of successive developmental stages are compared, a decreasing trend can be seen in the percentage C, N and H values, while the C:N ratio tended to increase.

Exuvial losses may be considered in relation to the larval or juvenile biomass reached shortly before ecdysis. Since the zoeal stages produced very thin and fragile exuviae with low contents of C, N and H, each of them lost only 3.4–3.8% of premoult dry mass and about 1–2% of premoult C, N and H. Much higher losses occurred in the megalopa, where 25% of premoult *W*, 5% of N, and 10% of C and H were lost. Yet higher losses were observed in the first juvenile crab stage which lost more than one half (53%) of total premoult *W*, 27% of C, 8% of N, and 13% of H.

In Fig. 5, exuvial losses are shown as percentage values of the initial biomass at hatching from the egg. This allows for separating exuvial from metabolic losses, which together are responsible for total losses occurring in individual biomass during the course of nonfeeding larval development. In the three zoeal stages combined, about 10% of the initial (posthatching) *W* and 4–5% of the initially available C, N and H were lost with the

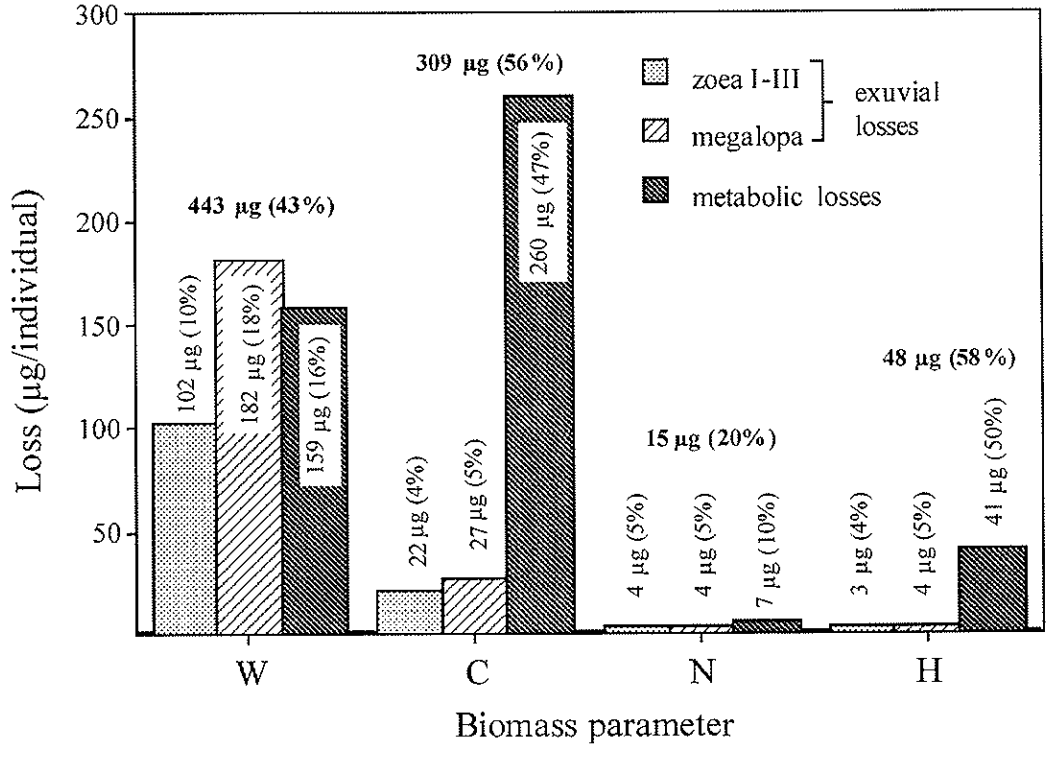

Fig. 5. *L. santolla*. Exuvial and metabolic losses of dry mass (*W*), carbon (C), nitrogen (N) and hydrogen (H) given in µg/individual and in % of the initially present biomass values at hatching.

shed exuviae. Another 18% of initial *W* and about 5% of C, N and H were lost with the megalopal exuvia cast at metamorphosis.

Total losses of biomass during lecithotrophic larval development from hatching to metamorphosis, including the combined effects of exuviation and metabolism, can be estimated as the difference between the initial biomass measured immediately after hatching (0 days) and those of the late megalopa (day 40, or 62 days after hatching; see Table 1; Fig. 2) after subtracting from this the biomass of the megalopal exuvia (Table 3). In *W*, C, N and H, these total losses amounted to ca. 443, 309, 14 and 48 μg/individual, or 43%, 56%, 20% and 58% of the initial (posthatching) values, respectively. Within these losses, the cast exuviae (all larval stages combined) accounted for about two thirds of *W* and one half of N lost from hatching to metamorphosis, while metabolic biomass degradation was responsible for most of the losses in C and H (Fig. 5).

4. Discussion

The patterns of larval and early juvenile development as well as changes in biomass and chemical composition observed in a Subantarctic king crab, *L. santolla*, can be compared with those previously described for a congener from the North Atlantic, *L. maja* (Anger, 1996). These two closely related but geographically separated subpolar species show a number of striking similarities not only in their adult ecology and climatic distribution but also in early development. Both pass through three zoeal stages and a megalopa, and comparison of development duration, larval survival, and changes in biomass and chemical composition of fed and unfed larvae shows that both species develop from hatching to metamorphosis completely independent from food. Total duration of larval development at 6 °C was about 10 weeks in *L. santolla*, while *L. maja* required about 7 weeks at a rearing temperature of 9 °C. This suggests similarity also in the temperature dependence of development duration.

The most striking similarity between *L. santolla* and *L. maja* is in the complete lecithotrophy from hatching through all four larval stages to metamorphosis. Both species live in subpolar regions where strong seasonality in the light conditions allows for only a short period of primary production, while low average temperatures, even during summer, enforce a long duration of development. This mismatch of short planktonic food availability and long pelagic development in cold waters should have selected for a food-independent mode of larval development, which is principally based on an enhanced energy allocation to female reproduction (for recent discussion, see Anger, 2001). Lecithotrophy has recently been observed also in a congener from the North Pacific and the Bering Sea, the golden king crab, *Lithodes aequispinus* (Shirley and Zhou, 1997), which suggests that this may be a wide-spread developmental pattern in *Lithodes* species living in high latitudes.

An extremely high C:N ratio (7.7) at hatching indicates that large lipid reserves persist in both species from the egg yolk, serving the larvae as an energy-rich fuel for endotrophic development under conditions of strongly limited food availability. In both species, the C:N ratio decreased significantly during larval development, which indicates a preferential

degradation of lipid reserves, especially during the zoeal (i.e. more active) phase of development, coinciding with a weaker decrease in the protein pool (cf. Anger, 1996). As another similarity between these species, the first juvenile crab stage showed immediately after metamorphosis food uptake and rapid growth. A particularly steep increase in the C:N ratio during the postmoult and early intermoult periods suggests a rapid replenishment of lost lipids. In addition, however, cuticular mineralization with inorganic carbonates may contribute to this increase in the C:N index. Decreasing values thereafter indicate in both species a proportionally stronger increase in the protein fraction, reflecting epidermal reconstruction and growth of muscular and nervous tissues during the premoult period. All these patterns are typical of planktotrophic larval and juvenile crab stages (for recent review, see Anger, 2001).

Besides the patterns of larval development and associated chemical changes within biomass, there are similarities in larval behaviour of these two *Lithodes* species. In the zoeal stages, both are slow but active swimmers, showing a tendency to stay near the bottom (demersal larvae). The same applies to the megalopa during the first 2–3 days after moulting. Subsequently, however, the megalopa becomes fully benthic and increasingly sluggish. Low locomotory activity of the larvae may be an energy-saving mechanism during nonfeeding development, representing another possible adaptation to food-limited environments.

As an additional tentatively adaptive trait, the larval stages (in particular the zoeae) of both species show very low exuvial energy losses as compared with planktotrophic decapod larvae (for recent discussion of the literature, see Anger, 1996, 2001). Production of unusually thin exuviae was observed also in a terrestrial brachyuran crab species with nonfeeding larvae (Anger and Schuh, 1992), suggesting that similar energy-saving traits may occur in various decapod crustacean taxa with a lecithotrophic mode of development.

Similar reproductive traits as in *Lithodes* spp. have recently been observed also in another Subantarctic lithodid species, the southern stone crab, *Paralomis granulosa* (Calcagno et al., submitted for publication a,b). This species shows a yet more abbreviated mode of development with only two zoeal stages and a megalopa. As in *L. santolla* and *L. maja*, its zoeae are demersal, while the megalopa is benthic and very inactive, and all larval stages are fully lecithotrophic. Likewise, endotrophic larval development is based on high initial energy stores remaining from the egg yolk (predominantly lipids), and a reduced locomotory activity and low exuvial losses of organic matter occur as putative energy-saving mechanisms. Together, these similarities suggest that such traits may be typical adaptations to conditions of short planktonic productivity in combination with low average temperatures in subpolar regions. Similar patterns may thus be expected to occur also in other lithodids from high latitudes, for instance, in *L. aequispinus*.

Acknowledgements

We greatly appreciate the help of the crew of PFS Polarstern during the transport of live king crabs. Special thanks are due to C. Püschel for elemental analyses. A. Chizzini and F.

Tapella helped in capturing specimens in the Beagle Channel. E. Heyer and R. Hottung helped in maintaining larval cultures. J. Calcagno is grateful to the German Academic Exchange Service (DAAD) for funding his research visit to Helgoland. This project was funded by the International Bureau of the German Ministry of Scientific Research (BMBF, project no. ARG 99/002), and the Argentine Secretaría Nacional para la Tecnología, Ciencia e Inovación Productiva (SETCIP). **[SS]**

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Vol. 253: 243–251, 2003 | MARINE ECOLOGY PROGRESS SERIES Mar Ecol Prog Ser | Published May 15

Larval and early juvenile development of *Paralomis granulosa* reared at different temperatures: tolerance of cold and food limitation in a lithodid crab from high latitudes

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ABSTRACT: *Paralomis granulosa* Jacquinot is a commercially fished lithodid crab species living in subantarctic and cold-temperate regions of southern South America. Its larval stages (Zoea I, II, Megalopa) are fully lecithotrophic, developing in the complete absence of food from hatching through metamorphosis; first feeding occurs in the first juvenile crab stage. In laboratory rearing experiments conducted at constant 1, 3, 6, 9, 12, and 15°C, we studied rates of larval and early juvenile survival and development in relation to temperature. At 1°C, many larvae (52%) reached the Megalopa stage almost 2 mo after hatching, but all died subsequently without passing through metamorphosis. Larval development was successfully completed at all other temperatures, with maximum survival at 6 to 9°C. The time of non-feeding larval development from hatching to metamorphosis lasted, on average, from 24 d (at 15°C) to almost 4 mo (117 d, at 3°C). When the experiment was terminated 1 yr after hatching, the 3rd (3°C) to 8th (15°C) juvenile crab instar had been reached. The relationship between the time of development through individual larval or juvenile stages (y) and temperature (T) was described as a power function ($y = a \times T^b$, or $\log[y] = \log[a] + b \cdot \log[T]$; the same regression model was also used to describe the temperature-dependence of cumulative periods of development from hatching. The wide thermal tolerance window for successful larval development (at least 3 to 15°C) and the broad geographic range of this species show that the early life-cycle stages of *P. granulosa* are cold-eurythermal. This physiological trait together with larval independence of food indicate that this lithodid crab species is well adapted to severe conditions of cold in combination with the food-limitation in subantarctic regions. Since similar traits have been also observed in other Lithodidae, we suggest that early life-history adaptations to low temperatures and low planktonic productivity may explain the high number of lithodid species occurring at high latitudes and in the deep sea, i.e. in conditions under which other Decapoda show strongly reduced diversity.

KEY WORDS: Lithodidae · *Paralomis granulosa* · Temperature · Larval development · Juvenile growth · Cold tolerance

INTRODUCTION

A macroecological pattern in the geographical distribution of higher animal and plant taxa is a decreasing trend in species diversity from low latitudes towards the poles (for recent review of the literature, examples, and discussion of relevant theories see Chown et al. 2000). Among the marine benthic invertebrates, this pattern has been particularly well documented for molluscs and crustaceans (e.g. Knox 1994, Clarke 1997, Crame & Clarke 1997). In a recent review of the distribution and life histories of temperate and antiboreal Decapoda of the SW Atlantic Ocean, Spivak (1997) listed a total of 243 species reported from the South

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American coasts from 25 to 55° S. Among these, only 37 species (15%) have been found in the southernmost region including Tierra del Fuego, the Falkland Islands (Islas Malvinas) and South Georgia (ca. 50 to 55° S). In another biogeographical review for the entire antiboreal region south of ~42° S (including the southern parts of the Atlantic, Pacific and Indian Oceans) Gorny (1999) listed 132 decapod crustacean species, with only 12 (9%) of these occurring south of the Antarctic Convergence. The impoverishment of the Antarctic decapod fauna during periods of climate cooling, about 20 million yr ago, is well documented in the fossil record also (Clarke 1993, Crame 1999, Stilwell & Feldmann 2000), indicating that declining temperatures and/or associated factors such as low productivity were critical factors in this process.

Besides food limitation in high-latitude environments (Knox 1994), physiological constraints to evolutionary cold adaptation are considered a principal cause of these patterns in biodiversity (Pörtner et al. 2000). In ectothermic animals in particular, their energetic metabolism appears to be affected by both unfavourably high and unfavourably low temperatures. When temperature drops below a species-specific critical level, insufficient aerobic capacity of the mitochondria leads to a shift towards an anaerobic mode of metabolism and, as a consequence, to an insufficient supply of cellular energy (for review of physiological mechanisms see Pörtner 2001, 2002). In most marine decapod taxa, this problem appears to be aggrevated by synergistic effects of Mg^{2+} ions, which reduce the scope for activity, especially at low temperatures (Frederich et al. 2000, 2001). Since the Decapoda and other marine invertebrates in high latitudes originated from warm-water ancestors (Arntz et al. 1994), the physiological problems typically faced under cold conditions require special evolutionary adaptations (Pörtner 2002), implying that relatively few, particularly adaptable, species may be successful.

Within the complex life cycles of decapod crustaceans and other marine invertebrates, the early (larval and juvenile) stages represent a physiological bottleneck, as they are generally more vulnerable to thermal, nutritional and other stress than the conspecific adults (for review see Anger 2001). In high latitudes, a mismatch of low water temperatures (causing long development times) and a short season of plankton production (implying lack of food throughout most of their pelagic development) should select against planktonic larvae. This may explain another macroecological pattern, namely a decreasing tendency in the number of species with planktonic larvae in latitudinal clines from warm to cold regions, i.e. 'Thorson's rule' (Thorson 1950; for recent discussion see Gallardo & Penchaszadeh 2001). While many species in high latitudes have evolved an abbreviated, often non-feeding mode of larval development (Gore 1985, Rabalais & Gore 1985, Anger 2001), others have completely supressed their planktonic larval phase. However, phylogenetic constraints may, in some taxa, prevent the evolution of an abbreviated or direct mode of development, so that the particular vulnerability of larvae may have contributed to the latitudinal gradients in biodiversity.

Despite severe problems associated with cold- and food-limited conditions in high latitudes, however, several decapod taxa have successfully adapted to Arctic or Antarctic biota (Christiansen & Christiansen 1962, Arntz & Gorny 1991, Arntz et al. 1997, 1999, Gorny 1999, Paul et al. 2002). In addition to some caridean shrimps and pagurid hermit crabs, this is most conspicuous in the distribution of stone crabs or king crabs (Lithodidae; for recent review see Zaklan 2002). In Spivak's (1997) species list, only 9 (3.7%) out of 243 decapod species recorded for the SW Atlantic region belong to this family, but 7 of these 9 (i.e. 78%) occur in the southernmost parts of this area, where they contribute about 19% to the regional decapod fauna. Similarly, 18 of 80 crab species recorded for the cold-temperate and subarctic waters of Alaska (22%) are lithodids (Stevens 2002), while warm-temperate and tropical decapod faunas show typically much lower proportions of stone crabs (for references see Dawson 1989). Moreover, recent observations have shown that lithodid crabs occur also in the extremely cold coastal waters of Greenland (Woll & Burmeister 2002) and in the high Antarctic Sea (Klages et al. 1995, Arana & Retamal 1999). It is thus not surprising that lithodids belong also to the most typical inhabitants of another cold- and food-limited environment, the deep sea (Chevaldonné & Olu 1996, Rex & Etter 1997, Gorny 1999, Zaklan 2002).

Since, as far as is known, the Lithodidae have several larval stages (McLaughlin et al. 2001, in press, and earlier papers cited therein), special adaptations to the conditions prevailing in high latitudes or in the deep sea are also required in their early life-history stages. Compared with other Anomura (including the closely related pagurid hermit crabs), lithodid crabs show tendencies towards an abbreviation of the pelagic larval phase and lecithotrophy, i.e. towards a food-independent mode of larval development (Anger 1996, Shirley & Zhou 1997, Lovrich et al. 2003). This holds true also for the subject of the present study, the subantarctic stone crab *Paralomis granulosa* Jacquinot. Recent observations on its larval development (comprising only 2 zoeal stages and a megalopa: Campodonico & Guzman 1981, McLaughlin et al. in press), larval survival and biochemical composition in laboratory cultures with and without food have shown that its

development from hatching to metamorphosis is fully endotrophic, being mainly based on a degradation of internal lipid reserves remaining from the egg yolk (Calcagno et al. in press, Kattner et al. in press).

Complete larval independence of external food sources may be considered a reproductive adaptation of *Paralomis granulosa* to conditions of low or seasonally brief productivity in subantarctic regions. In addition, in this species we would also expect larval adaptations to low temperatures. Since the zoeae hatch during the austral winter (Lovrich & Vinuesa 1999), they should be cold-tolerant, and their endotrophic potential should suffice for extended periods (weeks to months) of non-feeding development in the plankton. However, very little is known about the effects of temperature on the early life-history stages of this species. In a previous experimental study (Vinuesa et al. 1989), most larvae died in the zoeal stages, and metamorphosis from the megalopa to the first juvenile stage was not reached in any of the conditions tested (5 to 14°C).

In the present investigation on *Paralomis granulosa*, we studied the influence of temperature on survival and development of larvae and early juveniles, attempting to identify early life-history adaptations in this subantarctic species. Possible adaptive traits should also enhance our understanding of macroecological patterns such as latitudinal gradients in biodiversity, Thorson's rule, and the exceptional role of the Lithodidae within these patterns.

MATERIALS AND METHODS

The capture and maintenance of *Paralomis granulosa* as well as the rearing of their larvae are described in detail by Lovrich et al. (2003) and Calcagno et al. (in press). Briefly, ovigerous females were collected in April 2001 from the Beagle Channel (Tierra del Fuego, southern Argentina) using commercial fishing boats (for details of local crab fisheries see Lovrich 1997). They were kept in flow-through seawater aquaria at the local research institute (Centro Austral de Investigaciones Cientificas), and eventually transported with the German research icebreaker 'Polarstern' to the marine biological laboratory on Helgoland (Biologische Anstalt Helgoland), Germany. Subsequently, the crabs were maintained in flow-through seawater aquaria at a constant 6°C, ca. 32‰, and a 12:12 h light:dark cycle.

Freshly hatched, actively swimming larvae from 3 different females (A, B, C) were randomly selected and subsequently reared in individual 100 ml bowls kept under the same conditions of salinity and light. Since *Paralomis granulosa* releases only low numbers of larvae per night (normally <100, similar to the number reported for another lithodid species, *Lithodes maja*; see Anger 1996), we had to start 'parallel' experiments with different rearing temperatures using sibling larvae that hatched on different days. As rearing temperatures, we used 1, 3, 6, 9, 12 and 15°C; the lowest and the highest temperature, however, were tested only with larvae from 1 hatch (A). The initial number of larvae per treatment and hatch was n = 48, except for the experiment with Hatch B larvae reared at 9°C, where insufficient material allowed an initial number of only 46.

The larvae were reared without addition of food, since previous experiments (McLaughlin et al. 2001, in press, Calcagno et al. in press, Kattner et al. in press) had shown that all larval stages of *Paralomis granulata* are non-feeding. From the day of metamorphosis onwards, juvenile crabs were fed with *Artemia* sp. nauplii. At 9 to 15°C the culture water (and for juveniles also the food) was changed every other day; at lower temperatures the changes were made every third day. In all treatments, the larvae or juveniles were checked daily for moults or mortality.

The rearing experiments with 1 hatch (A) were continued throughout 1 yr, from August 2001 to August 2002, while all other experiments were terminated as soon as Crab Stage II was reached. Because of accidental loss of data, the experiment with Hatch A larvae reared at 12°C was prematurely terminated at Crab Stage III (instar stage), so no data were obtained for later juvenile stages in this group.

Our statistical analyses followed Sokal & Rohlf (1995). A 1-way ANOVA followed by comparisons between pairs of means was used for comparing survival and time of development at each larval stage. The durations of individual (larval or juvenile) stages as well as cumulative periods of development (e.g. from hatching to metamorphosis) are described as power functions of temperature (i.e. as linear regressions after log-transformation of both variables). Arithmetic mean values for different females rather than individual data were used as replicate values in the regression analyses. Slope parameters of the linearized regressions were compared with a test for heterogeneity of slopes using F statistics. Where average values with error estimates are given in the text or in figures and tables, these represent arithmetic mean values ± 1 SD.

RESULTS

Rates of survival

The survival of *Paralomis granulosa* through successive larval and juvenile stages varied greatly among temperatures and, at identical temperatures, among

hatches from different females (Table 1). Since the experiments with Hatches B and C were conducted only at 3 to 12°C and, moreover, terminated at Crab Stage II, the survival rates of different hatches can be compared only in this temperature range and only in the larval stages and in the first juvenile instar. For all larval stages, Hatch C showed lower survival than the other 2 hatches, except at 12°C. In contrast, Hatch A showed high survival of all larval stages, but high mortality at the first crab stage at 12°C and not at the other temperatures.

While the comparison among different hatches did not reveal a clear pattern, temperature was shown to have strong effects on survival. At the lowest temperature (1°C, tested only for Hatch A), 52% of the larvae survived through the 2 zoeal stages, but none of the survivors reached metamorphosis; i.e. complete mortality occurred at the Megalopa stage. The next higher temperature (3°C) allowed for 10 to 31% survival from hatching through metamorphosis in all hatches; however, complete mortality subsequently occurred at the first or second juvenile stage (Table 1). The highest level of survival was observed at 6°C, with a decreasing tendency at higher temperatures (accidental loss of data precluded inclusion of 12°C). When the experiments were terminated 1 yr after hatching, the survivors had maximally reached Juvenile Instars II (3°C), VI (6°C), VII (9°C), and VIII (15°C). Tables 1 to 3 show survival and development data for the latest juvenile instars near the end of the experiments only when all surviving individuals at a given temperature had reached these stages in August 2002. For instance, at 15°C, some crabs were at that time already in Juvenile Stage VIII, while others were still at Stage VI; in this case, the data for Stages VII and VIII were incomplete and thus not included in our tables or statistical analyses.

Rates of development

The development times of individual larval and juvenile stages are given in Table 2, the cumulative development times from hatching in Table 3. Among larvae originating from different females, statistically significant differences in individual stage durations were observed only in the 2 zoeal stages reared at 3 and 12°C. Variability among hatches often showed opposite tendencies in successive stages; e.g. Zoea I duration was shorter in Hatch A than in Hatch B, but Zoea II was longer in Hatch A than in Hatch B; Table 2). As a corollary, the cumulative durations to successive stages at identical temperatures were generally similar among the 3 hatches (no statistically significant differences: Table 3).

Increasing temperature had a clearly accelerating effect on development, especially in the lower temperature range. While an increase from 1 to 3°C or from 3 to 6°C caused a substantial decrease in moult-cycle duration in all stages, the differences observed between 12 and 15°C were mostly insignificant, the only exception being the Megalopa (Table 2). Within the temperature range tested in this study (1 to 15°C), the Zoea I lasted on average 3 to 17 d and Zoea II 4 to 39 d. The Megalopa stage (data available only for 3 to 15°C) lasted 17 to 84 d. Complete larval development from hatching to

Table 1. *Paralomis granulosa*. Rates of survival of individual developmental stages (% of survivors to a given stage) and cumulative survival from hatching to a given stage (as % of initial number at hatching [cum. %]). n = 46 for Female B at 9°C, n = 48 for all other experiments. Italics and bold-face: cumulative survival

T (°C)	Female	Zoea I %	Zoea II %	Zoea II cum.%	Megalopa %	Megalopa cum.%	Crab I %	Crab I cum.%	Crab II %	Crab II cum.%	Crab III %	Crab III cum.%	Crab IV %	Crab IV cum.%	Crab V %	Crab V cum.%	Crab VI %	Crab VI cum.%
1	A	90	58	***52***	0	***0***												
3	A	94	71	***67***	47	***31***	20	***6***										
	B	92	66	***60***	38	***23***	0	***0***										
	C	79	76	***44***	17	***10***	0	***0***										
6	A	98	89	***88***	95	***83***	90	***75***	100	***75***	94	***71***	100	***71***				
	B	90	86	***77***	89	***69***	79	***54***										
	C	96	70	***63***	59	***38***	58	***23***										
9	A	98	85	***83***	85	***71***	85	***58***	90	***54***	92	***50***	83	***42***	60	***25***	75	***19***
	B	98	78	***72***	71	***54***	100	***54***										
	C	100	90	***90***	81	***73***	89	***54***										
12	A	98	94	***83***	86	***58***	53	***4***	10									
	B	96	84	***77***	54	***42***	70	***29***										
	C	96	61	***58***	46	***27***	92	***25***										
15	A	98	94	***83***	82	***73***	50	***38***	67	***25***	92	***23***	91	***21***	70	***15***	57	***8***

Table 2. *Paralomis granulosa*. Duration of development (d) of successive larval and juvenile stages from 3 different females (A, B, C) at different temperatures

T (°C)	Female	Zoea I x	±SD	Zoea II x	±SD	Megalopa x	±SD	Crab I x	±SD	Crab II x	±SD	Crab III x	±SD	Crab IV x	±SD	Crab V x	±SD	Crab VI x	±SD
1	A	16.9	(1.1)	39.2	(2.7)														
3	A	7.8	(1.7)	26.9	(2.8)	83.7	(2.4)	102.3	(11.0)										
	B	9.7	(1.5)	25.5	(1.6)	82.0	(3.2)												
	C	9.6	(1.3)	21.6	(1.8)	85.8	(1.9)												
6	A	5.2	(0.5)	10.9	(0.5)	39.2	(2.2)	48.4	(3.0)	55.8	(6.4)	75.5	(15.6)	88.4	(15.4)				
	B	5.3	(0.5)	10.9	(0.5)	37.8	(1.9)	47.4	(3.5)										
	C	5.6	(1.3)	10.3	(1.0)	38.8	(1.8)	45.6	(4.0)										
9	A	3.4	(0.5)	6.3	(0.6)	31.6	(2.3)	33.8	(2.6)	37.0	(3.2)	50.6	(6.2)	53.3	(6.9)	74.8	(12.5)	74.4	(17.7)
	B	3.5	(0.5)	5.8	(0.6)	28.6	(2.8)	35.1	(2.5)										
	C	3.4	(0.5)	6.2	(0.4)	32.0	(2.7)	33.4	(1.9)										
12	A	3.0	(0.0)	4.9	(0.3)	23.0	(2.5)	24.1	(8.8)	29.5	(0.7)								
	B	4.0	(0.0)	3.5	(0.5)	22.2	(1.8)	28.0	(2.9)										
	C	4.0	(0.0)	3.5	(0.5)	24.1	(1.4)	27.4	(1.7)										
15	A	3.0	(0.0)	4.1	(0.5)	17.4	(1.6)	26.4	(2.7)	28.4	(4.8)	32.9	(5.2)	39.9	(8.9)	43.7	(4.3)	53.0	(12.8)

Table 3. *Paralomis granulosa*. Cumulative time of development (days from hatching) to successive larval and juvenile stages from 3 different females (A, B, C) at different temperatures

T (°C)	Female	Megalopa x	±SD	Crab I x	±SD	Crab II x	±SD	Crab III x	±SD	Crab IV x	±SD	Crab V x	±SD	Crab VI x	±SD	Crab VII x	±SD
1	A	56.3	(2.8)														
3	A	34.6	(3.2)	117.4	(2.7)	219.0	(9.5)										
	B	34.8	(1.3)	115.9	(3.8)												
	C	30.5	(1.5)	115.4	(2.0)												
6	A	16.0	(0.4)	55.2	(2.4)	103.7	(4.6)	154.4	(8.4)	218.5	(19.1)	266.3	(11.6)				
	B	16.2	(0.7)	54.0	(2.0)	101.5	(4.5)										
	C	15.8	(0.7)	48.9	(2.0)	99.6	(3.7)										
9	A	9.6	(0.5)	41.2	(2.5)	75.4	(3.7)	112.0	(5.5)	163.0	(8.2)	217.3	(13.1)	291.6	(21.2)	356.7	(16.7)
	B	9.3	(0.5)	37.9	(2.7)	73.0	(4.5)										
	C	9.6	(0.5)	41.5	(2.7)	74.7	(4.0)										
12	A	7.9	(0.3)	30.8	(2.9)	64.0	(5.7)										
	B	7.5	(0.5)	29.8	(1.8)	57.9	(3.9)										
	C	7.5	(0.5)	31.5	(1.2)	58.8	(1.9)										
15	A	7.1	(0.5)	24.3	(1.6)	50.6	(3.3)	78.7	(7.7)	112.0	(9.8)	150.6	(15.4)	188.4	(12.4)	240.5	(20.2)

metamorphosis took from 24 d at 15°C to 117 d at 3°C, i.e. from 3.5 wk to almost 4 mo (Table 3).

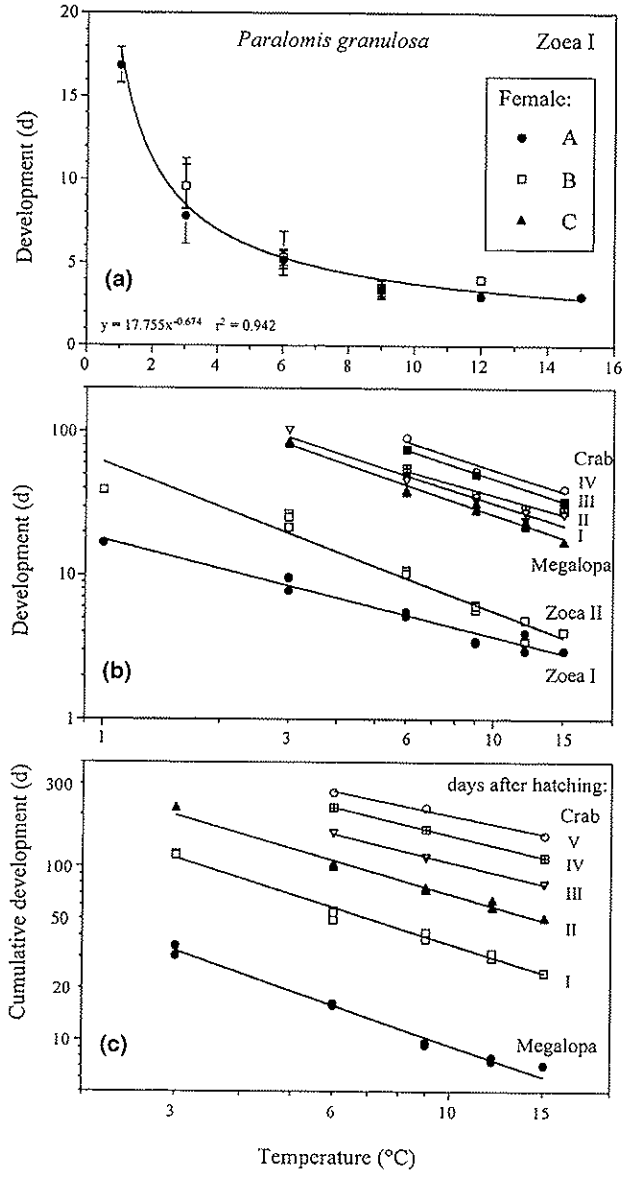
The moult-cycle duration of successive juvenile instars also showed a clear decrease with increasing temperature; e.g. the duration of Crab Stage I varied from 26 d at 15°C to 102 d at 3°C. As another consistent trend, the young crab stages showed increasing moult-cycle durations in successively later instars. At 15°C, for example, Crab Stage I lasted on average 26 d, while Crab Stage VI was about twice as long (53 d).

The patterns of development duration (y, days) in relation to temperature (T, °C) could generally be described with a best fit between observed and predicted data when a power function was used as a model: $y = a \times T^b$, with a and b being fitted constants; all coefficients of determination, $R^2 > 0.9$ (Table 4). Only the data for Zoea Stage II fitted better with a logarithmic function: $y = -33.1 \times \log[T] + 38.9$; $R^2 = 0.959$; the power function yielded in this case $R^2 = 0.929$); however, since this was the only exception, herein we consistently use the power function as a general model of developmental temperature-dependence for individual stages as well as for cumulative development times from hatching to successively later stages. The fitted regression parameters and R^2 coefficients are compiled in Table 4.

These non-linear patterns are illustrated in Fig. 1a using the untransformed Zoea I data as an example.

Table 4. *Paralomis granulosa*. Fitted parameters (a, b) and coefficients of determination (R^2) of non-linear regression equations (power functions, $y = a \times T^b$) describing development time (y, days) as a function of temperature (T, °C). Dev/stage: time of development in individual stages; Cum. dev: cumulative time of development from hatching to later stages

Parameter	Zoea I	Zoea II	Megalopa	Crab I	Crab II	Crab III	Crab IV	Crab V
Dev/stage								
a	17.8	61.3	223.4	237.4	210.0	376.6	386.4	
b	−0.674	−1.036	−0.925	−0.874	−0.765	−0.904	−0.855	
R^2	0.942	0.929	0.983	0.958	0.952	0.998	0.951	
Cum. dev								
a		17.8	103.2	316.5	515.7	569.9	808.6	832.2
b		−0.674	−1.048	−0.950	−0.874	−0.734	−0.730	−0.626
R^2		0.942	0.986	0.986	0.980	0.999	0.999	0.990



The linearized regressions (after log-log transformation) are shown in Fig. 1b for all individual stages for which complete data for a minimum of 3 different temperatures were available (i.e. from Zoea I to the Crab IV; cf. Table 2). The cumulative development duration in relation to temperature is shown in Fig. 1c. The slopes of these regression lines were not significantly different from each other (ANCOVA, $p > 0.05$), indicating a similar degree of temperature-dependence for successive developmental stages.

DISCUSSION

Perhaps the most striking result of this study is the wide range of temperatures tolerated by larval and early juvenile stone *Paralomis granulosa*. At a temperature as low as 1°C, about one-half of the larvae developed successfully to the megalopa stage, and metamorphosis to the first juvenile crab stage was reached within a tolerance window from 3 to 15°C. This suggests that the complete mortality before metamorphosis observed in a previous study (Vinuesa et al. 1989) was not caused by unsuitable temperatures but probably was due to either weakness of the larval material or poor rearing conditions.

In the area of origin of our material, the Beagle Channel, the larvae of *Paralomis granulosa* hatch in winter (July and August: Lovrich & Vinuesa 1999), when the water temperature is near its average annual minimum (5.4°C: Lovrich 1999). Since our experimental data suggest an optimum of about 6 to 9°C, the larvae and juveniles of this species appear to be optimally

Fig. 1. *Paralomis granulosa*. Duration of larval and early juvenile development in relation to temperature. (a) Non-linear relationship (power function), Zoea I stage at 1 to 15°C; (b) development of successive stages (Zoea I to Crab IV); (c) cumulative development duration from hatching to successive stages (Megalopa to Crab V)

adapted to the regional climate near Tierra del Fuego. According to the regional water temperatures in winter and spring, and considering our present results, the larvae should become megalopae 2 to 3 wk after hatching (late July and August), and metamorphosis to the first juvenile crab would be expected to occur throughout September to November. In the following winter, 1 yr after hatching from the egg, the juveniles should approximately reach Crab Instars VI to VII.

At 1°C we observed successful development to the Megalopa and larval survival for about 2 mo, suggesting that this species is well adapted to tolerate more severe conditions of cold than those occurring in the Beagle Channel. Theoretically, this capability might enable *Paralomis granulosa* to occasionally cross the Drake Passage and invade Antarctic waters, although the prevailing current patterns would probably favour an indirect immigration via South Georgia rather than a direct route (see Knox 1994, his Fig. 11.8). With continued global warming, *P. granulosa* may thus be considered a pioneer candidate for a possible recolonization of the Antarctic shelf by reptant decapods. However, earlier invaders may be found among the cold-stenothermal deep-sea lithodids.

The average maximum summer temperature reached in the Beagle Channel is 9.8°C (Lovrich 1999). Again, this shows that the tolerated range for larval development in *Paralomis granulosa* is much wider than would be required within the region of origin of our material. This tolerance of relatively warm conditions (up to at least 15°C) indicates that *P. granulosa* is not really a typical 'cold-adapted', i.e. cold-stenothermal, but actually a cold-eurythermal species (cf. Pörtner et al. 2000, Pörtner 2002). This is consistent with its broad geographic distribution in the subantarctic region and along both sides of southern South America, ranging in the Atlantic north to Santa Catarina, Brazil (Boschi et al. 1992), and in the Pacific to the Island of Chiloé, Chile (Retamal 1981). Likewise, this response pattern is congruent with the observation that *P. granulosa* is the only species of its genus that also inhabits shallow coastal waters where temperatures may be quite variable (Macpherson 1988).

The thermal response pattern of the early life-history stages of *Paralomis granulosa* may be typical of those Lithodidae (or at least of *Paralomis* and *Lithodes* spp.) that live in high latitudes, commonly with wide ranges of geographic and bathymetric distribution (for references see Paul et al. 2002). In contrast, true deep-sea species living in a more stable environment should be cold-stenothermal. Since our observations show that the larvae and juveniles of *P. granulosa* are cold-eurythermal, they should be an interesting object for testing the physiological hypotheses of thermal tolerance recently proposed by Pörtner (2001, 2002). These hypotheses suggest that this species, including its early life-history stages, should be capable of regulating its mitochondrial densities and/or its energetic capacity in response to seasonal, bathymetric, or regional changes in temperature, or after differential acclimatization in the laboratory.

With regard to extremely long periods of larval development at low temperature (<6°C), it should be stressed that during this time no intake of food occurs, and development depends solely on the utilization of internal energy reserves. Although an extended lecithotrophic period under cold conditions indicates low rates of metabolic consumption, successful non-feeding development over a period of up to 4 mo remains highly remarkable, since metabolic disturbance below a critical temperature leads to insufficient cellular oxygen and energy supplies (Pörtner 2001, 2002), which may eventually prevent effective utilization of internal energy reserves. When larvae of warm-temperate crab species were simultaneously exposed to unfavourably low temperatures and an absence of food, they died sooner than sibling larvae starving at higher temperatures, although metabolic energy demands increase at higher temperatures, and thus one would expect shorter survival times in warmer waters (Anger et al. 1981).

In summary, our study has shown that *Paralomis granulosa* is well adapted to thrive under the conditions of food limitation and cold found in high-latitude marine ecosystems. On the other hand, it is equally well adapted to cool temperate regions, where relatively elevated temperature levels exclude truly cold-adapted stenothermal species. Thus, a remarkable larval eurythermal ability together with an unusually high endotrophic potential allow extended periods of completely food-independent development from hatching through metamorphosis in this species.

Similar patterns were also observed in a stone crab from the North Atlantic, *Lithodes maja* (Anger 1996), as well as in a Pacific congener, *L. aequispinus* (Shirley & Zhou 1997). In the latter species, the maximum period of non-feeding larval development (148 d at 3°C: Paul & Paul 1999) even exceeds, by 1 mo, the maximum time observed in *Paralomis granulosa*. Successful larval development at 9°C as well as a wide geographic distribution (from Japan to the Bering Sea, Canada and Alaska: Zaklan 2002) suggest that, like *P. granulosa*, *L. aequispinus* is a eurythermal rather than a cold-stenothermal species.

The occurrence of ovigerous females of *Lithodes maja* in coastal waters of Greenland, where water temperatures between −1 and 5°C were recorded (Woll & Burmeister 2002) suggests cold resistance in the early life-history stages of this species similar to that in *Paralomis granulosa* and (probably) *L. aequispinus*. Al-

though no data on temperature effects are available for larvae of *L. maja*, a longer development from hatching to metamorphosis (about 50 d at 9°C: Anger 1996) than in *P. granulosa* (38 to 42 d) suggests that *L. maja* also passes through a very long non-feeding larval development at low temperatures. In this species also, the early life-history stages are not cold-stenothermal but eurythermal, as reflected by its wide geographic distribution from the southern North Sea to Spitzbergen, Iceland and Greenland (Zaklan 2002).

These patterns contrast with those of the commercially more important lithodid *Paralithodes camtschatica*. Although this species also occurs at high latitudes (Stevens 2002, Sundet & Hjelset 2002) and its larvae tolerate a wide range of temperatures, from low to moderately high (0 to 15°C: Shirley & Shirley 1989), its zoeae are known to require planktonic food (e.g. Kurata 1960, Paul & Paul 1980); however, its megalopa stage is secondarily lecithotrophic (see Abrunhosa & Kittaka 1997a,b).

While these comparisons of larval tolerance of cold and food limitation show that not all lithodid crabs occurring at high latitudes have reached the same degree of adaptation to thermally and nutritionally harsh conditions, similarities among the various species suggest that a combination of larval eurythermality and lecithotrophy may be a widespread trait in lithodids. Phylogenetic constraints in other reptant Decapoda may not generally allow for an evolution of such special adaptations and may thus have contributed to both gradients of decreasing species diversity and to the tendency towards a reduction of the larval phase with increasing latitude ('Thorson's rule').

Acknowledgements. We greatly appreciate the help of the crew of PFS 'Polarstern' during the transport of live crabs. U. Nettelmann and several students helped in maintaining larval and juvenile cultures. J.C. is grateful to the German Academic Exchange Service (DAAD, Bonn) and the Alfred-Wegener-Institut für Polar- und Meeresforschung (Bremerhaven) for funding his research visits to Helgoland. This project was funded by the International Bureau of the German Ministry of Scientific Research (BMBF, project no. ARG 99/002), and the Argentine Secretaría Nacional para la Tecnología, Ciencia e Inovación Productiva (SETCIP).

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Editorial responsibility: Otto Kinne (Editor), Oldendorf/Luhe, Germany

Submitted: December 17, 2002; Accepted: February 6, 2003
Proofs received from author(s): April 22, 2003

Polar Biol (2003) 26: 279–282
DOI 10.1007/s00300-002-0476-6

SHORT NOTE

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First record of anomuran and brachyuran larvae (Crustacea: Decapoda) from Antarctic waters

Received: 10 September 2002 / Accepted: 17 December 2002 / Published online: 7 February 2003

Abstract Two decapod crustacean larval morphotypes belonging to the Anomura and Brachyura were found for the first time in Antarctic waters. Nine specimens were obtained from qualitative plankton hauls in Maxwell Bay (Bransfield Strait) (62°14'33S; 58°43'81W) off King George Island, Antarctic Peninsula. The anomuran morphotype belonged to the Hippidae, and apparently to the genus *Emerita*, whereas the brachyuran representative was assigned to the genus *Pinnotheres* (Pinnotheridae). At present, species determination is not possible due to lack of knowledge of larval morphology in both families. Adult forms of these reptant decapods are not known from Antarctic waters; the occurrence of the present larval forms is considered as a possible intrusion of Subantarctic water masses into the Antarctic environment. This hypothesis is supported by the additional presence of the copepod genus *Acartia* in the same sample material, which is exclusively known from Subantarctic waters.

Introduction

Diversity of decapod crustaceans in the higher latitudes of both hemispheres has been frequently shown to be outstandingly low (Yaldwyn 1965; Abele 1982; Briggs 1995). In the Antarctic, the impoverishment in decapod fauna is assumed to be a result of Antarctic cooling during the formation of the Antarctic Circumpolar Current (ACC), a process that may have ended about 23 Ma ago (for review see Barker et al. 1991; Crame 1999; see also Lawver et al. 1992). Recently, the benthic decapod fauna of the Antarctic regime is represented by only about a dozen benthic, natant species (Yaldwyn 1965; Kirkwood 1984; Tiefenbacher 1990; Thatje 2003). However, some anomuran lithodid species were recently found in deeper waters off the continental shelf of the Antarctic Bellingshausen Sea (Klages et al. 1995; Arana and Retamal 2000), suggesting that the southern limits of reptants and the distribution-limiting ecophysiological processes involved are not well defined.

In the present study, two reptant larval morphotypes obtained from a plankton haul taken in Antarctic Maxwell Bay off King George Island (62°14'33S, 58°43'81W, Fig. 1) are described. This first record of anomuran and brachyuran larvae in Antarctic waters is discussed, taking into account biogeography and oceanographic aspects.

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Materials and methods

Sampling of plankton material was carried out on a weekly basis (January to April 2002) in Maxwell Bay (62°14'33S, 58°43'81W, Fig. 1) off King George Island. Qualitative surface samples from the upper water layer (about 10 m depth to surface) were obtained by means of a Bongo net of 200 µm mesh, towed by an inflatable dinghy (1 km transect). Samples were preserved in 3% formalin solution buffered with hexamethylenetetramine, and later transferred into 70% ethanol. Anomuran and brachyuran larvae were only obtained from the sample taken on 28 March. Carapace (CL) and total lengths (TL) of the larvae were measured from the base of the rostrum between the eyes to the posterior dorsal margin of the carapace, and to the posterior margin of the telson, respectively. Dissection of the decapod larval material was done using a Zeiss stereomicroscope.

Results

Larval morphology

Anomura: Hippidae: *Emerita sp.*

Early zoea, five specimens, TL = 1.25 mm, CL = 0.52 mm (Fig. 2A–C)

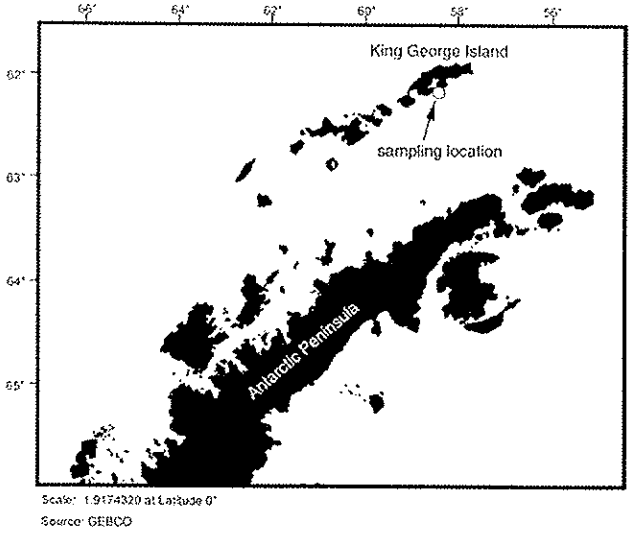

Fig. 1 Sampling location of anomuran (Hippidae) and brachyuran (Pinnotheridae) larvae in Maxwell Bay (62°14'33S; 58°43'81W) off King George Island, Antarctic, in March 2002

General characteristics Carapace smooth, colourless; eyes conspicuously stalked and directing laterally, reaching beyond margin of carapace (Fig. 2A, B); rostrum with wide base and rounded tip, directing anterior-ventrally (Fig. 2A, B); abdomen of four short, smooth segments (Fig. 2A), last segment with lateral posterior expansion; telson as wide as long, posteriorly rounded margin with 30 short spines, central ones larger in size; one pair of posteriolateral short spines present (Fig. 2C); antennae pointing and much longer than rostrum; first and second maxillipeds very similar; exopod of elongated segment slightly longer than endopod; short terminal segment with four long, plumose setae (Fig. 2A).

Remarks The larvae reveal morphological attributes of the genus *Emerita* (compare with, e.g., Johnson and Lewis 1942; Knight 1967). The present species seems to be related to *Emerita brasiliensis*; both have a strong similarity in telson setation, including the posterolateral pair of spines (compare with Veloso and Calazans 1993). However, the extremely broad base and rounded tip of the rostrum (Fig. 2A, B) and the posterolateral expansion of the last abdominal segment (Fig. 2C) may discard all close relations, suggesting the present larval material belongs to an unknown hippid (see also Rees 1959).

Brachyura: Pinnotheridae: *Pinnotheres* sp.

Early zoea, two specimens, TL = 1.08 mm, CL = 0.46 mm (Fig. 2D, E)

Advanced zoea, two specimens, TL = 2.14 mm, CL = 0.88 mm (Fig. 2F)

General characteristics Eyes sessile; carapace with long dorsal and one pair of lateral spines (about half as long as dorsal spine), directing postero-ventrally (Fig. 2D);

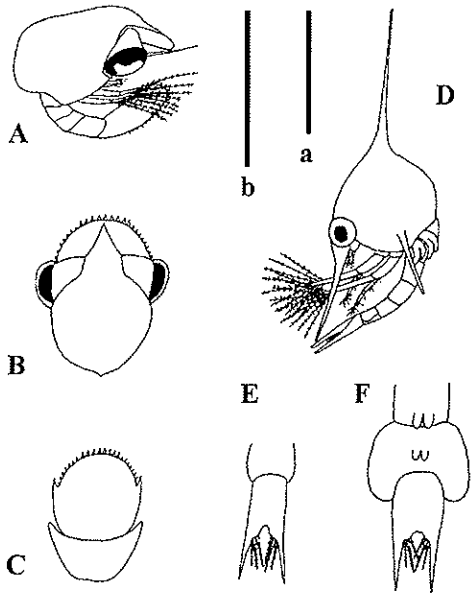

Fig. 2A–F Decapod crustacean morphotypes found in Maxwell Bay (62°14'33S; 58°43'81W) off King George Island (Antarctica) in March 2002. Anomura: Hippidae (**A** – **C**), **A** lateral view; **B** dorsal view; **C** telson, dorsal view; Brachyura: Pinnotheridae (**D** – **F**), **D** lateral view of early zoea; **E** telson of early zoea; **F** telson of advanced zoea. Scale bars: *a* = 0.5 mm (**D**), *b* = 0.75 mm (**A** – **C**, **E**, **F**)

rostral spine slightly shorter than dorsal spine; first and second maxillipeds very similar in morphology; elongated segment of exopod with ten terminal feathered setae, slightly longer than endopod; endopod of five segments; abdomen of four segments, smooth; advanced zoea with pleopodal buds on all somites (Fig. 2F), which are absent in early morphotype; last segment of pleon with lateral expansions (Fig. 2E; more developed in advanced zoea, Fig. 2F); telson with strong furca and medial cleft, and long distinct furcal spines, more developed in advanced zoea (compare Fig. 2E, F); telson with three setose spines on each furca; both larval stages with rudimentary pereiopodal buds.

Remarks The above general characteristics identify the larval material as belonging to the genus *Pinnotheres* within the Pinnotheridae (compare with Saelzer and Hapette 1986; Pohle et al. 1999). Due to great similarity in morphology, both morphotypes are assumed to belong to the same species (see also Costlow and Bookhout 1966; Roberts 1975).

Discussion

Biogeographic origin of larvae

The Pinnotheridae and Hippidae occur in the intertidal to shallow subtidal of sandy beaches (Roberts 1975;

Saelzer and Hapette 1986), an environment virtually absent from the Antarctic. The southernmost records of the genus *Pinnotheres* of the Atlantic and Pacific coasts off South America are reported for northern Argentina (Mar del Plata, 38°S) and the island of Chiloe (42°S; Retamal 1981). Hippidae usually occur in warmer waters, their southernmost distribution in America being northern Chile and southern Brazil (Retamal 1981; Boschi et al. 1992). However, *E. analoga* Stimpson, 1857, has been found in the Strait of Magellan and Tierra del Fuego (about 52°S; Efford 1976; Boschi et al. 1992), although these rare finds have not been confirmed by recent investigations (Gorny 1999). We were not able to assign both reptant larval morphotypes to the species-level, due to the limited knowledge of larval morphology of both families. It is likely that the larvae described are related to species from South America, which is closest to the Antarctic Peninsula.

Intrusion of water masses into the Antarctic regime?

The Antarctic Circumpolar Current (ACC), including the Polar Front, is assumed to be the principal physical barrier for plankton organisms. Antezana (1999) suggested that the occasional appearance of Antarctic plankton organisms in the Subantarctic Magellan region may be explained by Antarctic cold-water rings, which are generated from meanders at the Polar Front (for discussion see Joyce and Patterson 1977; Joyce et al. 1981; Nowlin and Klinck 1986). A probable more impacting oceanographic feature could be the superficial breach of the ACC by water masses (for discussion see Li et al. 2002). We assume similar oceanographic phenomena to be responsible for our present find of reptant decapod larvae in Antarctic waters. Since reptant decapods are virtually absent from the Antarctic (Gorny 1999; Frederich et al. 2001), and the reptant larvae found in our samples were associated with specimens of the Subantarctic copepod genus *Acartia*, these hints are further indications of an introduction of Subantarctic plankton into the Antarctic regime. The intrusion of Subantarctic warm-water rings south of the Polar Front may serve as a homogeneous environment for the transported plankton community (Nowlin and Klinck 1986) and may, therefore, allow survival and further larval development, and could explain the appearance of more advanced pinnotherid larvae in our samples. The fact that the reptant larvae and Subantarctic copepods were associated with some typical Antarctic copepod representatives, such as *Metridia gerlachei*, *Calanus propinquus*, *Calanoides acutus* and *Rincalanus gigas*, indicates a mixture of water masses in our sampling area.

The occurrence of anomuran and brachyuran larvae in Antarctic waters suggests that breach of the Antarctic Counter Current is possible and is a possible transport mechanism for plankton organisms.

Acknowledgements The second author is indebted to the German Academic Exchange Service (DAAD) for financing her scientific stay in Germany, and to Sigrid Schiel for providing working facilities at the Alfred Wegener Institute, Germany. Our thanks are due to the Argentine staff of the Antarctic Jubany station at King George Island for help and assistance in the field during the summer of 2001/2002. Danilo Koetz Calazans was a great help in identifying the decapod larvae. We are indebted to Alexander Tzetlin and three anonymous reviewers for their helpful comments on the manuscript.

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5 ACKNOWLEDGEMENTS

First of all, I especially wish to thank my family and friends who supported me during the last years and who often suffered from my hardly understandable restless way of life.

I am indebted to all the institutional support I received during the last years, which allowed for completing the present work: the Alfred Wegener Institute, Bremerhaven, and the Biologische Anstalt Helgoland, for providing working facilities in Bremerhaven and Helgoland as well as the research platforms RVs Polarstern and Uthörn; to the German Academic Exchange Service (DAAD) for supporting the cooperation with my Argentine counterparts, to the SEPCYT (Argentina) and the International Bureau of the BMBF (DLR) for supporting the Argentine-German bilateral cooperation during the last years, and to the Volkswagen Foundation for funding one preparative scientific stay in Chile.

I would like to thank my supervisor Prof. Dr. Wolf Arntz who made this work possible. I am grateful for his support of my research projects and especially my sometimes very "pragmatic" travel methods, and for his unlimited support of my scientific exploration of the remote world of South America – thank you for your confidence and the freedom in developing my own way!

Dr. Klaus Anger picked me up somewhen on my way through South America, I think it was in Buenos Aires. Thank you, Klaus, for your great support of my work, our fruitful co-operation, and most important your friendship. I would like to thank Prof. Dr. Andrew Clarke for taking over the "Zweitgutachter" in a very final stage of this work.

Fruitful science mainly depends on a good team and working atmosphere. This work would not have been possible without my colleagues and friends from South America, as well as German cooperation partners: Dr. Gustavo A. Lovrich, Dr. Javier A. Calcagno, Silvana Sede, Dr. Rosa Bacardit, Dr. Federico Tapella, Carolina Romero, Mirta Lovrich, Sofía and Augustin, Dr. Klaus Anger, Prof. Dr. Wilhelm Hagen, Dr. Franz-Josef

Sartoris, Uwe Nettelmann, as well as many others I apologise for not having mentioned here.

In this context, I would especially like to thank Dipl. Phys. Matthias Hermes and his former team from DLR-International Bureau (BMBF) for the outstanding flexibility in supporting my work in South America and Germany. Without this help and most important continuity in severe days of Argentine political and economic crises (only insider can really understand that), my work would have been hardly possible.

Related to this topic, Dr. Rainer Paulenz and AWI helped me filling one financial gap when it was urgently needed.

Thank you to Dr. Axel Bachmann for taxonomic discussion. Thank you also to many colleagues and/or friends from AWI and elsewhere for the fruitful discussions and companionship in Bremerhaven, and at conferences and expeditions during the last years: Dr. habil. Sigrid Schiel, Prof. Dr. Hans-Otto Pörtner, Dr. Barbara Niehoff, Ingo Fetzer, Astrid Cornils, Nuria Teixidó, Dr. Enrique Isla, Dr. Jürgen Laudien, Sabine Grabbert, Dr. Hendrik Deubel, Elke Barwich, Detlef Barwich, Kerstin Beyer, Fabian Vanella, Uwe Nettelmann, José Velez, Ruth Alheit, Americo Montiel, Andrea Bleyer, Antonio Baeza, Dr. Patricio Manriquez, Dr. Betina Lomovasky, Dr. Anne-Nina Lörz, Dr. Katrin Linse, Dr. Martin Rauschert, Dr. Claus-Dieter Hillenbrand, Dr. Franz-Josef Sartoris, Petra Wencke, Gabriela Torres, Dr. Luis Giménez, Oscar Gonzales, Lucas Ruberto, Dr. habil Doris Abele, Dr. Dieter Gerdes, Dr. habil. Thomas Brey.

I am indebted to the masters and crews of the RVs Polarstern and Uthörn for help and assistance at sea, and especially during the crab transports from South America to the small island in the North Sea. Thanks also to all these tasty crabs and tiny little larvae for having supported my work.

I am most grateful to my family and especially my mother, Karin Thatje, for their unlimited support of my dreams in life.

Neptune released MS Bremen

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