

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

S. Thatje\*, S. Schnack-Schiel, W. E. Arntz

Alfred Wegener Institute for Polar and Marine Research, PO Box 120 161, 27515 Bremerhaven, Germany

**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

*Resale or republication not permitted without written consent of the publisher*

## 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 infra-order 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-

\*Email: [sthatje@awi-bremerhaven.de](mailto:sthatje@awi-bremerhaven.de)

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 planktonic 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  $\mu\text{m}$  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<sup>2</sup>).

**Species identification and larval developmental mode.** The meroplankton frac-

tion 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

- Planktonic 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,

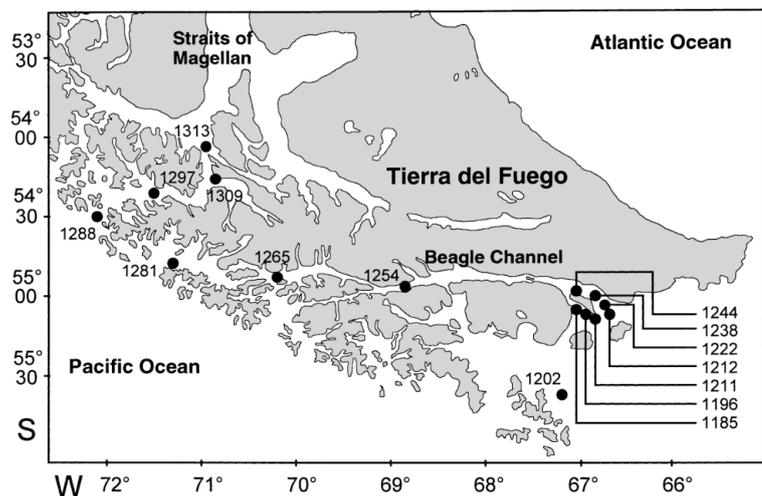


Fig. 1. Meroplankton sampling locations (black dots/station numbers) during the Joint Chilean-German-Italian Magellan 'Victor Hensen' Campaign to the Magellan region (South America) in November 1994

Table 1. Station means (ind. m<sup>-3</sup>) 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	–	–
<b>Decapoda</b>																
<b>Thalassinidea</b>																
<i>Notiax</i> sp. (?)	Zoea 1	–	–	–	–	–	–	30	1440	9224	20	35	30	6424	3756	240
	Zoea 2	–	–	–	–	–	–	–	127	3076	–	–	–	520	1808	13
<i>Upogebia</i> sp.	Decapodid	–	–	–	–	–	–	–	7	–	–	–	–	–	8	–
<b>Brachyura</b>																
Pinnotheridae	Early zoea	4	–	–	2	–	–	3	100	–	–	–	–	–	36	–
<i>Libidoclaea granaria</i>	Zoea 1	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–
<i>Eurypodius latreillei</i>	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	–
<i>Peltarion spinosulum</i>	Zoea 1	–	–	13	–	–	–	13	–	4	133	–	5	4	–	147
	Zoea 2	–	–	–	–	–	7	–	–	8	33	–	–	–	–	7
<i>Halicarcinus planatus</i>	Zoea 1	–	–	–	36	–	–	–	53	–	–	5	–	8	12	–
	Zoea 2	–	–	–	–	–	–	–	–	–	–	–	–	4	–	–
<b>Anomura</b>																
<i>Pagurus</i> 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
<i>Parapagurus dimorphus</i> (?)	Early zoea	–	–	–	–	–	–	–	–	–	–	–	5	20	4	–
	Adv. zoea	–	–	–	–	–	–	–	–	–	–	–	–	–	8	–
<i>Munida</i> 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	–	–	–	–	–
<b>Caridea</b>																
<i>Betaeus truncatus</i>	Zoea 1	–	–	–	–	–	–	–	–	–	7	–	–	–	–	–
<i>Eualus dozei</i>	Zoea 1	–	–	–	–	–	–	–	7	–	–	–	–	–	–	–
<i>Campylonotus vagans</i>	Zoea 1	–	–	–	–	–	–	–	–	–	–	10	–	–	–	–
	Zoea 2	–	–	–	–	–	–	–	–	–	–	10	–	8	–	–
	Decapodid	–	–	–	–	–	–	–	–	–	–	–	–	–	40	–
<i>C. semistriatus</i>	Decapodid	22	–	–	–	–	–	–	–	–	–	–	–	–	–	–
<i>Nauticaris magellanica</i>	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	–	–
<i>Austropandalus grayi</i>	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	–
<b>Astacidea</b>																
<i>Thymops birsteini</i>	Decapodid	–	13	–	–	–	22	–	–	8	–	–	–	–	–	–
<b>Palinura</b>																
<i>Stereomastis (suhmi)</i> (?)	Early zoea	–	–	–	–	22	–	–	7	–	–	–	–	–	8	–
	Adv. zoea	–	–	–	–	22	–	–	–	–	–	10	–	–	–	–
Sum		11 455	2424	11 283	13 075	4729	928	6195	8610	15 224	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

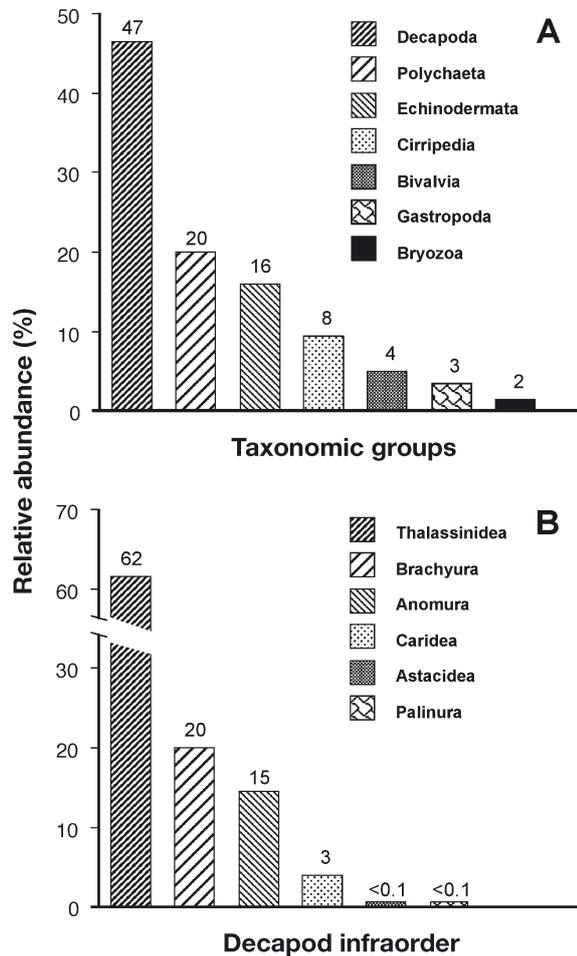


Fig. 2. Relative abundance of meroplankton fractions found in the channel and fjord system of the Magellan region in November 1994. Given on the basis of (A) major taxonomic groups and (B) decapod infraorder

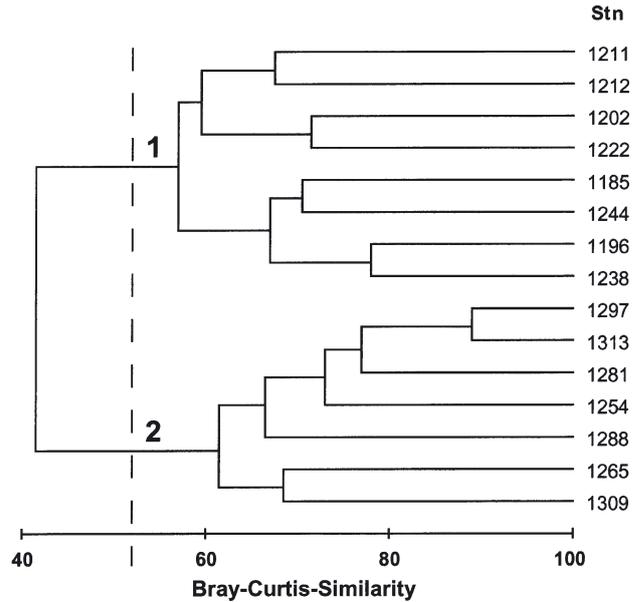


Fig. 3. Cluster dendrogram (Bray-Curtis similarity) showing classification of meroplankton stations on the basis of abundance means

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 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 echi-

noderns 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.

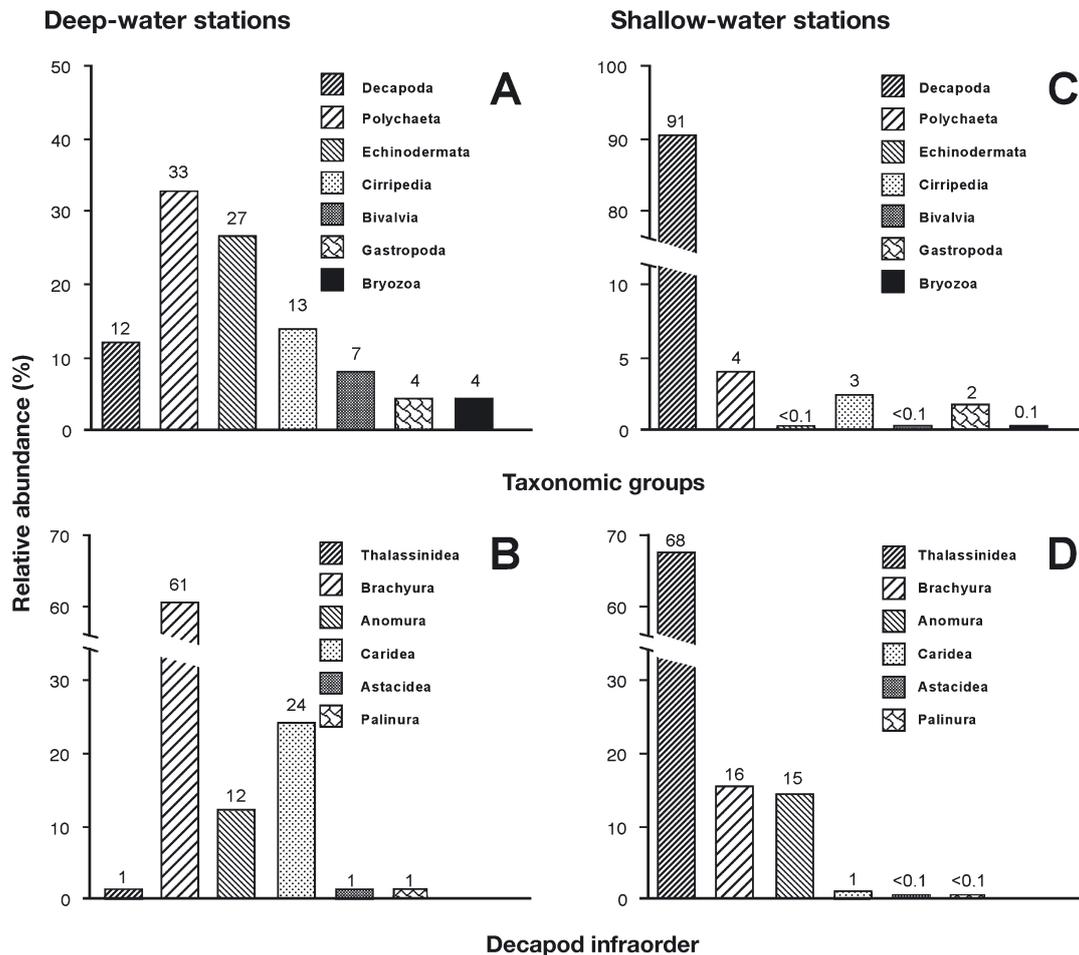


Fig. 4. Relative abundance of meroplankton fractions found in the channel and fjord system of the Magellan region in November 1994. Comparison of deep-water station means (A,B) with that of shallow-water stations. Given on the basis of (A,C) major taxonomic groups, (B,D) decapod infraorder

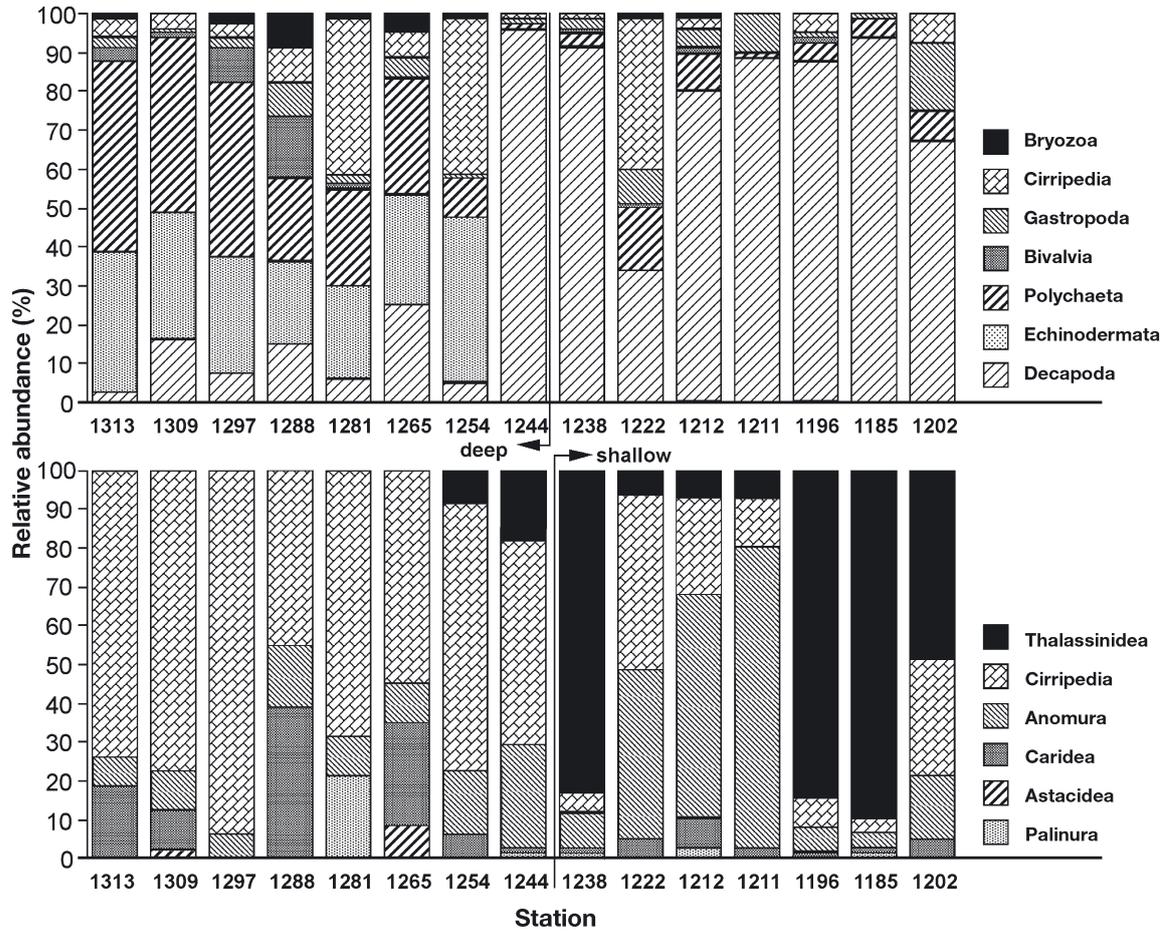


Fig. 5. Relative abundance of meroplankton fractions found at each station sampled in the Magellan region in November 1994. Given on the basis of (A) major taxonomic groups, (B) decapod infraorder

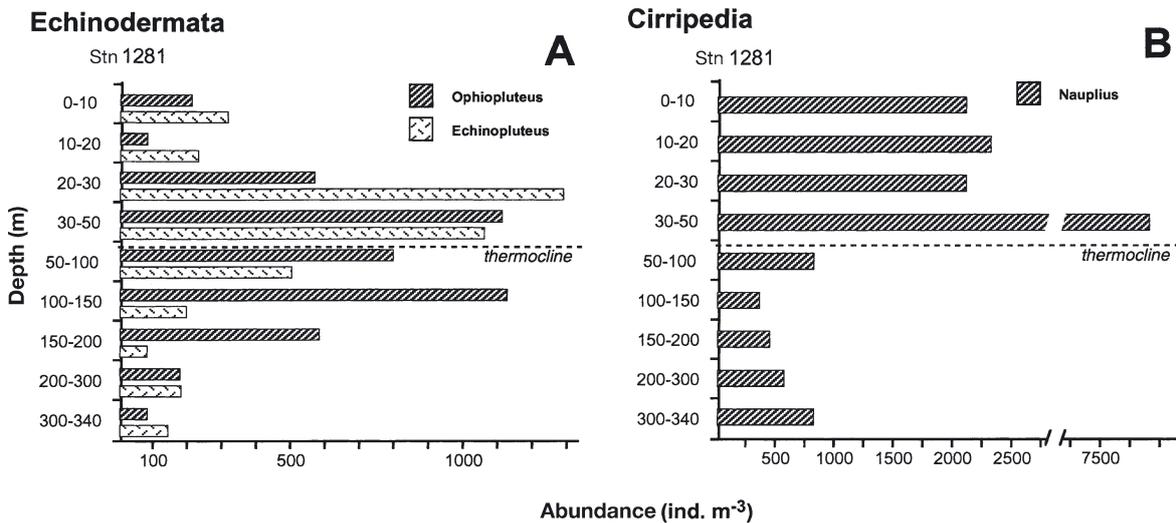


Fig. 6. Vertical distribution of echinoderm and cirripede larvae at Stn 1281. Dotted line = thermocline (at 70 to 80 m water depth, see Antezana et al. 1996)

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.

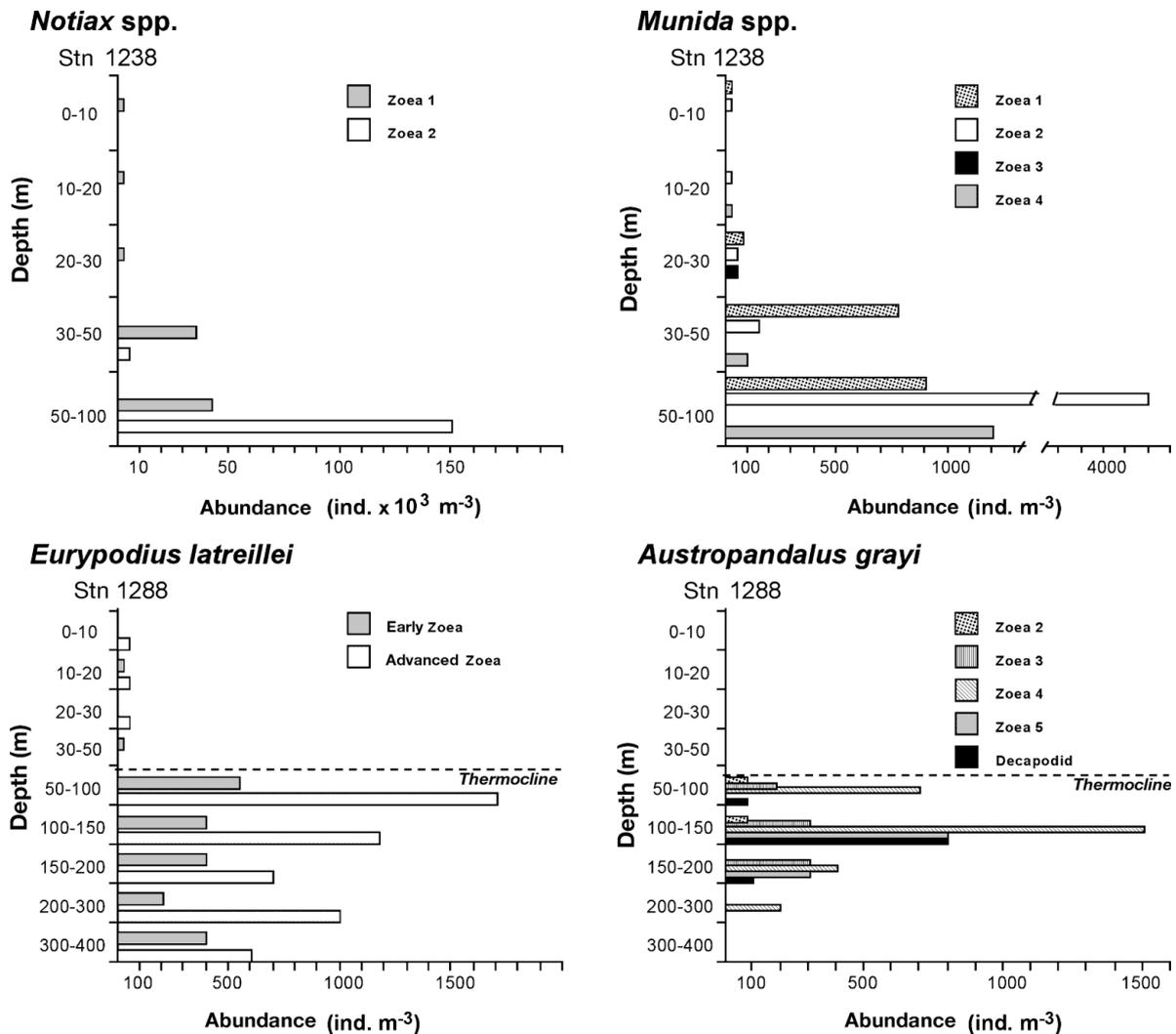


Fig. 7. Vertical distribution of selected decapod taxa from different sampling stations; *Notiax* sp. (Stn 1238), *Munida* spp. (Stn 1238), *Eurypodius latreillei* (Stn 1288), *Austropandalus grayi* (Stn 1288). Dotted line = thermocline (at 80 to 90 m water depth, see Antezana et al. 1996)

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	Abbreviated	Plankto- trophic	Lecitho- trophic	Plank- tonic	Demersal	
<b>Caridea</b>							
<i>Campylonotus vagans</i> Bate, 1888		x	x		x		28, 30
<i>Campylonotus semistriatus</i> Bate, 1888		x	x		x		28
<i>Chorismus antarcticus</i> (Pfeffer, 1887)		x	x		x		6, 19
<i>Chorismus tuberculatus</i> Bate, 1888		x	x		x		26
<i>Betaeus truncatus</i> Dana, 1852		?	x		x		1, 29
<i>Eualus dozei</i> (A. Milne Edwards, 1891)		?					1
<i>Nauticaris magellanica</i> A. Milne Edwards, 1891		x	x		x		1, 27, 33, 34
<i>Austropandalus grayi</i> (Cunningham, 1871)	x		x		x		25
<b>Palinura</b>							
<i>Stereomastis (suhmi)</i> Bate, 1878, (?)						x	21
<b>Anomura</b>							
<i>Munida subrugosa</i> Henderson, 1847	x		x		x		17, 22, 32, 35, 36
<i>Munida gregaria</i> (Fabricius, 1793)	x		x		x		17, 32, 35, 36
<i>Lithodes santolla</i> (Molina, 1782)		x		x		x	7, 9, 16, 18, 19
<i>Paralomis granulosa</i> (Jaquinot, 1847)		x		x		x	7, 8, 10, 16, 20
<i>Pagurus comptus</i> White, 1847	x		x		x		17, 23, 24, 31
<i>Pagurus forceps</i> H. Milne Edwards, 1836	x		x		x		17, 23, 24, 31
<i>Parapagurus (dimorphus)</i> Smith, (?)						x	3, 21
<b>Brachyura</b>							
<i>Eurypodius latreillei</i> Guérin, 1828		x	x		x		2, 4, 11, 17
<i>Libidoclaea granaria</i> (H. Mil. Edw. & Lucas, 1842)	x		x		x		4, 12, 17
<i>Halicarcinus planatus</i> (Fabricius, 1775)	x		x		x		5, 17
<i>Peltarion spinosulum</i> (White, 1843)	x		x		x		14, 17
<i>Pinnixia</i> sp.		?	x		x		13, 17
<i>Cancer edwardsi</i> Bell, 1835	x		x		x		15
<b>Astacidea</b>							
<i>Thymops birsteini</i> (Zarenkov & Semenov, 1972)						?	21
<b>Thalassinidea</b>							
<i>Notiax</i> sp. (?)						x	21
Sources							
(1) Albornoz & Wehrtmann (1997)	(13) Gutierrez-Martinez (1971)				(25) Thatje & Bacardit (2000a)		
(2) Bacardit (1985b)	(14) Iorio (1983)				(26) Thatje & Bacardit (2000b)		
(3) Bacardit (1985a)	(15) Quintana (1983)				(27) Thatje & Bacardit (2000c)		
(4) Bacardit & Vera (1986)	(16) Kattner et al. (2003)				(28) Thatje et al. (2001)		
(5) Boschi et al. (1969)	(17) Lovrich (1999)				(29) Thatje & Bacardit (2001)		
(6) Bruns (1992)	(18) Lovrich et al. (2003)				(30) Thatje & Lovrich (2003)		
(7) Calcagno et al. (2003a)	(19) McLaughlin et al. (2001)				(31) Thatje & Lovrich (unpubl.)		
(8) Calcagno et al. (2003b)	(20) McLaughlin et al. (2003)				(32) Vera & Bacardit (1986)		
(9) Campodonico (1971)	(21) Present study				(33) Wehrtmann & Albornoz (1998)		
(10) Campodonico & Guzman (1972)	(22) Roberts (1973)				(34) Wehrtmann & Kattner (1998)		
(11) Campodonico & Guzman (1981)	(23) Scelzo & Boschi (1969)				(35) Williams (1973)		
(12) Fagetti (1969)	(24) Scelzo (1976)				(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 echinoderms, 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, Wehrmann & 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 (Wehrmann 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 men-

tioned 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.

#### LITERATURE CITED

- Albornoz L, Wehrtmann IS (1997) Descripción y clave de los primeros estadios larvales de camarones carideos (Decapoda: Hippolytidae, Alpheidae, Rhynchocinetidae) de aguas costeras de Chile. *Invest Mar Univ Catol Valparaíso* 25:121–133
- Anger K (2001) The biology of decapod crustacean larvae. *Crustacean issues*, Vol 14. A.A. Balkema, Lisse
- Anger K, Schuh M (1992) Bioenergetics of abbreviated larval development in the bromelid crab, *Metopaulias depressus* (Decapoda: Grapsidae). *Comp Biochem Physiol A* 103: 507–518
- Anger K, Dawirs RR, Anger V, Goy JW, Costlow JD (1981) Starvation resistance in first stage zoeae of brachyuran crabs in relation to temperature. *J Crustac Biol* 1:518–525
- Anger K, Thatje S, Lovrich GA, Calcagno JA (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. *Mar Ecol Prog Ser* 253:243–251
- Antezana T, Hamamé M, Eissler Y, Jara S (1996) Hydrography in Chilean fjords: Strait of Magellan to Beagle Channel (legs 1 and 2). In: Arntz W, Gorny M (eds) *Cruise report of the Joint Chilean-German-Italian Magellan 'Victor Hensen' Campaign in 1994*. *Ber Polarforsch* 190:16–18
- Arana PM, Retamal MA (2000) Nueva distribución de *Paralomis birsteini* Macpherson 1988 en aguas antártidas (Anomura, Lithodidae, Lithodinae). *Invest Mar Univ Catol Valparaíso* 27:101–110
- Arntz WE, Gili JM (2001) A case for tolerance in marine ecology: Let us not put out the baby with the bathwater. *Sci Mar* 65(Suppl 2):283–299
- Arntz W, Gorny M (1996) *Cruise report of the Joint Chilean-German-Italian Magellan 'Victor Hensen' Campaign in 1994*. *Ber Polarforsch* 190:1–113
- Arntz WE, Brey T, Gerdes D, Gorny M, Gutt J, Hain S, Klages M (1992) Patterns of life history and population dynamics of benthic invertebrates under the high Antarctic conditions of the Weddell Sea. In: Colombo G, Ferrari I, Ceccherelli VU, Rossi R (eds) *Marine eutrophication and population dynamics*. *Proc 25th Europ Mar Biol Symp*. Olsen & Olsen, Fredensborg, p 221–230
- Bacardit R (1985a) Larvas de Crustacea Decapoda del Atlantico sudoccidental. I. Primer estadio larval del genero *Parapagurus* Smith (Anomura, Parapaguridae). *Physis (Buenos Aires) Secc A* 43(105):73–77
- Bacardit R (1985b) Larvas de crustacea Decapoda del Atlantico sudoccidental. II. Morfología de las larvas y postlarvas de *Eurypodius latreillei* Guerin (Brachyura, Majidae), provenientes de muestras de plancton del Mar Argentino. *Physis (Buenos Aires) Secc A* 43(105):79–89
- Bacardit R, Vera V (1986) Larvas de Crustacea Decapoda del Atlantico sudoccidental. III. Distribución y abundancia de larvas y postlarvas de *Eurypodius latreillei* Guerin y *Lipidoclaea granaria* Milne-Edwards y Lucas (Brachyura, Majidae) en el Mar Argentino. *Physis (Buenos Aires) Secc A* 44(106):9–20
- Boschi EE, Scelzo MA, Goldstein B (1969) Desarrollo larval del cangrejo *Halicarcinus planatus* (Fabricius) (Crustacea, Decapoda, Hymenosomidae), en el laboratorio, con observaciones sobre la distribución de la especie. *Bull Mar Sci* 19(1):225–242
- Brambati A, Fontolan G, Simeoni U (1991) Recent sediments and sedimentological processes in the Strait of Magellan. *Boll Oceanol Teor Applic* 9(2-3):217–259
- Bruns T (1992) Experimentelle Untersuchungen zur Larvalentwicklung antarktischer Garnelen (Decapoda, Natantia). Diplomarbeit, Universität Osnabrück, (unpublished MSc thesis)
- Calcagno JA, Lovrich GA, Anger K, Thatje S, Kaffenberger A (2003a) Larval development in the Subantarctic king crabs *Lithodes santolla* (Molina) and *Paralomis granulosa* (Jaquinot) reared in the laboratory. *Helgol Mar Res* 57: 110–113
- Calcagno JA, Thatje S, Anger K, Lovrich GA, Kaffenberger A (2003b) Changes in biomass and chemical composition during lecithotrophic larval development of the southern stone crab, *Paralomis granulosa*. *Mar Ecol Prog Ser* 257: 189–196
- Campodonico I (1971) Desarrollo larval de la centolla *Lithodes antarctica* Jacquinot en condiciones de laboratorio (Crustacea Decapoda, Anomura: Lithodidae). *An Inst Patagonia Ser Cienc Nat* 2:181–190
- Campodónico IG, Guzman LM (1972) Desarrollo larval de *Eurypodius latreillei* Guerin en condiciones de laboratorio. *An Inst Patagonia Ser Cienc Nat* 3(1/2):233–247
- Campodónico I, Guzman L (1981) Larval development of *Paralomis granulosa* (Jaquinot) under laboratory conditions (Decapoda, Anomura, Lithodidae). *Crustaceana* 40: 278–285
- Clarke A (1982) Lipid synthesis and reproduction in polar shrimps. *Mar Ecol Prog Ser* 9:81–90
- Clarke A (1988) Seasonality in the Antarctic marine environment. *Comp Biochem Physiol B* 90:461–473
- Clarke A (1990) Temperature and evolution: Southern Ocean cooling and the Antarctic marine fauna. In: Kerry KR, Hempel G (eds) *Antarctic ecosystems. Ecological change and conservation*. Springer Verlag, Berlin, p 9–22
- Clarke KR, Gorley RN (2001) *Primer V.5: user manual/tutorial*. Primer-E, Plymouth
- Cunningham CW, Blackstone NW, Buss LW (1992) Evolution of king crabs from hermit crab ancestors. *Nature* 355: 539–542
- Defren-Jansen K, Schnack-Schiel SB, Richter C (1999) Meso-

- zooplankton communities in the Magellan region. *Sci Mar* 63(Suppl 1):43–50
- Dyers MF (1985) The distribution of *Hyas araneus* (L.) and *Hyas coarctatus* Leach (Crustacea: Decapoda: Brachyura) in the North Sea and the Svalbard region. *J Mar Biol Assoc UK* 65:195–201
- Fagetti E (1969) The larval development of the spider crab *Libidoclaea granaria* H. Milne Edwards & Lucas under laboratory conditions (Decapoda Brachyura; Majidae, Pisinae). *Crustaceana* 17:131–140
- Feldmann RM, Tshudy DM (1989) Evolutionary pattern in macrurus decapod crustaceans from Cretaceous to Early Cenozoic rocks of the James Ross Island region, Antarctica. In: Crame JA (ed) *Origins and evolution of the Antarctic biota*, Vol 47. Geological Society, London, p 183–195
- Frederich M, Sartoris FJ, Pörtner HO (2001) Distribution patterns of decapod crustaceans in polar areas: a result of Magnesium regulation? *Polar Biol* 24:719–723
- Gorny M (1999) On the biogeography and ecology of the Southern Ocean decapod fauna. *Sci Mar* 63(Suppl 1): 367–382
- Gorny M, George MR (1997) Oocyte development and gonad production of *Nematocarcinus lanceopes* (Decapoda: Caridea) in the eastern Weddell Sea, Antarctica. *Polar Biol* 17:191–198
- Gorny M, Arntz WE, Clarke A, Gore DJ (1992) Reproductive biology of caridean decapods from the Weddell Sea. *Polar Biol* 12:111–120
- Gutiérrez-Martínez J (1971) Notas biológicas sobre *Pinnaxodes chilensis* (M. Edwards) y descripción de su primera Zoea (Crustacea, Decapoda, Anomura). *Mus Nac Hist Nat Mens (Santiago)* 176:3–10
- Iorio I (1983) Estadios larvales del cangrejo *Peltarion spinosulum* (White) (Crustacea, Decapoda, Brachyura, Ateleocy-clidae). *Physis (Buenos Aires) Secc A* 41(101):143–156
- Kattner G, Graeve M, Calcagno JA, Lovrich GA, Thatje S, Anger K (2003) Lipid, fatty acid and protein utilization during lecithotrophic larval development of *Lithodes santolla* (Molina) and *Paralomis granulosa* (Jacquinot). *J Exp Mar Biol Ecol* 292:61–74
- Klages M, Gutt J, Starmans A, Bruns T (1995) Stone crabs close to the Antarctic continent: *Lithodes murrayi* Henderson, 1888 (Crustacea; Decapoda; Anomura) off Peter I Island (68° 51' S, 90° 51' W). *Polar Biol* 15:73–75
- Lovrich GA (1999) Seasonality of larvae of Brachyura and Anomura (Crustacea Decapoda) in the Beagle Channel, Argentina. *Sci Mar* 63(Suppl 1):347–354
- Lovrich GA, Thatje S, Calcagno JA, Anger K, Kaffenberger A (2003) Changes in biomass and chemical composition during lecithotrophic larval development of the Southern king crab, *Lithodes santolla* (Molina). *J Exp Mar Biol Ecol* 288:65–79
- Macpherson E (1988) Three new species of *Paralomis* (Crustacea, Decapoda, Anomura) from the Pacific and Antarctic oceans. *Zool Scr* 17:69–75
- Magalhães C (1988) The larval development of palaemonid shrimps from the Amazon region reared in the laboratory. II. Extremely abbreviated larval development in *Euryrhy-nchus* Miers, 1877 (Decapoda, Euryrhynginae). *Crustaceana* 55:39–52
- Makarov RR (1968) On the larval development of the genus *Sclerocrangon* GO Sars (Caridea, Crangonidae). *Crustaceana* 2(Suppl):27–37
- McLaughlin PA, Lemaitre R (2000) Aspects of evolution in the anomuran superfamily Paguroidea: one larval perspective. *Invertebr Reprod Dev* 38(3):159–169
- McLaughlin PA, Anger K, Kaffenberger A, Lovrich GA (2001) Megalopal and early juvenile development in *Lithodes santolla* (Molina, 1782) (Decapoda: Anomura; Paguroidea: Lithodidae), with notes on zoeal variations. *Invertebr Reprod Dev* 40:53–67
- McLaughlin PA, Anger K, Kaffenberger A, Lovrich GA (2003) Larval and early juvenile development in *Paralomis granulosa* (Jacquinot) (Decapoda: Anomura; Paguroidea: Lithodidae), with emphasis on abdominal changes in megalopal and crab stages. *J Nat Hist* 37:1433–1452
- Miglavls IJ (1992) *Sclerocrangon boreas*, the sculptured shrimp: a new species for mariculture. Some primary results of cultivation. 1st Eur Crustac Conf Paris (31 Aug to 5 Sep 1992) Abstracts. *Mus Nat Hist Nat, Paris*, p 99
- Mileikovskiy SA (1971) Types of larval development in marine bottom invertebrates, their distribution and ecological significance: a re-evaluation. *Mar Biol* 10:193–213
- Montú M, Anger K, Bakker C (1990) Variability in the larval development of *Metsasarma rubripes* (Decapoda, Grapsidae) reared in the laboratory. *Neritica* 5(1):113–128
- Odinetz Collart O, Magalhães C (1994) Ecological constraints and life history strategies of palaemonid prawns in Amazonia. *Verh Internat Verein Limnol* 25:2460–2467
- Pearse JS, McClintock JB, Bosch I (1991) Reproduction of Antarctic benthic marine invertebrates: tempos, modes, and timing. *Am Zool* 31:65–80
- Pérez-Barros P, Tapella F, Romero MC, Calcagno JA, Lovrich GA (in press) Benthic decapod crustaceans associated to captures of *Munida* spp. (Decapoda: Anomura) in the Beagle Channel, Argentina. *Sci Mar*
- Pörtner HO (2002) Climate variations and the physiological basis of temperature dependent biogeography: systemic to molecular hierarchy of thermal tolerance in animals. *Comp Biochem Physiol A* 132:739–761
- Quintana R (1983) Larval development of the edible crab, *Cancer edwardsi* Bell, 1835, under laboratory condition (Decapoda, Brachyura). *Rep USA Mar Biol Inst Kochi Univ* 5:1–19
- Roberts PE (1973) Larvae of *Munida subrugosa* (White 1847), from Perseverance Harbour, Campbell Island. *J R Soc NZ* 3(3):393–408
- Romero MC, Tapella F, Lovrich GA, Thatje S (2003) Reproductive modes and distribution of benthic decapod crustaceans along the Scotia Arc. *Ber Polarforsch* (in press)
- Scelzo MA (1976) Larvas de los crustaceos decapodos anomuros, identificadas en las aguas marinas Argentinas. *Physis (Buenos Aires) Secc A* 35(90):37–45
- Scelzo MA, Boschi EE (1969) Desarrollo larval del cangrejo ermitaño *Pagurus exilis* (Benedict) en laboratorio (Crustacea, Anomura, Paguridae). *Physis (Buenos Aires) Secc A* 29(78):165–184
- Schubart CD, Diesel R, Hedges SB (1998) Rapid evolution to terrestrial life in Jamaican crabs. *Nature* 393:363–365
- Thatje S (2000) *Notiax santarita*, a new species of the Callianasidae (Decapoda, Thalassinidea) from the Beagle Channel, southernmost America. *Crustaceana* 73(3):289–299
- Thatje S, Bacardit R (2000a) Larval development of *Austropandalus grayi* (Cunningham, 1871) (Decapoda: Caridea: Pandalidae) from the southwestern Atlantic Ocean. *Crustaceana* 73(5):609–628
- Thatje S, Bacardit R (2000b) Larval stages of *Chorismus tuberculatus* (Decapoda: Caridea: Hippolytidae) from the southwestern Atlantic Ocean. *J Mar Biol Assoc UK* 80:465–471
- Thatje S, Bacardit R (2000c) Morphological variability in larval stages of *Nauticaris magellanica* (A. Milne Edwards, 1891) (Decapoda: Caridea: Hippolytidae) from South American waters. *Bull Mar Sci* 66(2):375–398
- Thatje S, Bacardit R (2001) Two zoeal stages of *Betaeus trun-*

- catus* (Dana, 1852) (Decapoda: Caridea: Alpheidae) from Argentine coastal waters. An Inst Patagonia Ser Cienc Nat 29:95–104
- Thatje S, Gerdes D (2000) *Upogebia australis*, a new species of the Upogebiidae (Crustacea, Decapoda, Thalassinidea) from the Beagle Channel (Magellan Region). Mitt Mus Naturkunde Berlin, Zool Reih 76(2):231–236
- Thatje S, Lovrich GA (2003) Decapodid and early juvenile development in the protandrous shrimp *Campylonotus vagans* Bate, 1888 (Crustacea: Decapoda), with notes on larval morphology. J Mar Biol Assoc UK 83(1):103–109
- Thatje S, Bacardit R, Romero MC, Tapella F, Lovrich GA (2001) Description and key to the zoeal stages of the Campylonotidae (Decapoda, Caridea) from the Magellan Region. J Crustac Biol 21(2):492–505
- Thatje S, Calcagno JA, Lovrich GA, Sartoris FJ, Anger K (2003) Extended hatching periods in the Subantarctic lithodid crabs *Lithodes santolla* and *Paralomis granulosa* (Crustacea: Decapoda). Helgol Mar Res 57:110–113
- Thatje S, Lovrich GA, Anger K (in press a) Egg production, hatching rates, and abbreviated larval development of *Campylonotus vagans* Bate, 1888 (Crustacea: Decapoda: Caridea) in subantarctic waters. J Exp Mar Biol Ecol
- Thatje S, Lovrich GA, Torres G, Hagen W, Anger K (in press b) Changes in biomass, lipid, fatty acid and elemental composition during the abbreviated larval development of the subantarctic shrimp *Campylonotus vagans* Bate, 1888. J Exp Mar Biol Ecol
- Thorson G (1936) The larval development, growth and metabolism of Arctic marine bottom invertebrates compared with those of other seas. Medd Gronl 100:1–155
- Thorson G (1950) Reproductive and larval ecology of marine bottom invertebrates. Biol Rev 25:1–45
- Vera V, Bacardit R (1986) Larvas de Crustacea Decapoda del Atlantico sudoccidental. IV. Nuevas larvas del genero *Munida* Leach. (Anomura, Galatheididae). Physis (Buenos Aires) Secc A 44(107):59–66
- Wehrtmann IS (1991) How important are starvation periods in early larval development for survival of *Crangon septemspinosa* larvae? Mar Ecol Prog Ser 73:183–190
- Wehrtmann IS, Albornoz L (1998) Larval development of *Nauticaris magellanica* (A. Milne Edwards, 1891) (Decapoda: Caridea: Hippolytidae), reared under laboratory conditions. Bull Mar Sci 62(1):45–72
- Wehrtmann IS, Kattner G (1998) Changes in volume, biomass, and fatty acids of developing eggs in *Nauticaris magellanica* (Decapoda: Caridea): a latitudinal comparison. J Crustac Biol 18(3):413–422
- Williams BG (1973) The effect of the environment on the morphology of *Munida gregaria* (Fabricius) (Decapoda, Anomura). Crustaceana 24:197–210
- Williams BG (1980) The pelagic and benthic phases of post-metamorphic *Munida gregaria* (Fabricius) (Decapoda, Anomura). J Exp Mar Biol Ecol 42:125–141
- Williamson DI (1982) Larval morphology and diversity. In: Abele LG (ed) The biology of Crustacea, Vol 2. Embryology, morphology, and genetics. Academic Press, New York, p 43–110
- Zinsmeister WJ, Feldmann RM (1984) Cenozoic high latitude heterochroneity of southern hemisphere marine faunas. Science 224:281–283

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

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