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# Monobrachium parasitum (Cnidaria: Hydrozoa) epizoic on antarctic bivalves and its bipolarity

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Jarms, G. & U. Mühlenhardt-Siegel. *Monobrachium parasitum* (Cnidaria: Hydrozoa) epizoic on antarctic bivalves and its bipolarity.

Zool. Verh. Leiden 323, 31.xii.1998: 125-139, figs 1-4, tabs 1-5.— ISSN 0024-1652/ISBN 90-73239-68-0. G. Jarms & U. Mühlenhardt-Siegel, Zoologisches Institut und Zoologisches Museum, Universität Hamburg, Martin-Luther-King Platz 3, 20146 Hamburg, Germany.

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During antarctic macrozoobenthos research, colonies of *Monobrachium* were found on small bivalves. The species problem of the genus *Monobrachium* is discussed and it is stated that there are three species. However, the widespread species *Monobrachium parasitum* might be a species-complex comprising several species. This can only be confirmed by rearing experiments and/or molecular investigations. Host specificity and the factors influencing the infection of the bivalve species are shown. The impact of the infection is demonstrated to be harmful to the host bivalve, although not of a parasitic nature. The phenomenon of bipolarity within the genus *Monobrachium* is discussed.

# Introduction

For 20 years antarctic macrozoobenthos has been the aim of qualitative and quantitative investigations. Since 1984 the benthos of the Scotia Arc was the subject of special investigations (Hartmann, 1986, 1987, 1988; Mühlenhardt-Siegel, 1988, 1989). In order to analyse benthic associations, their diversity and dominance in both abundance and biomass, quantitative samples were taken. Special attention was paid to small species among the zoobenthos to examine the biogeography of some meiofaunal groups, especially ostracods and small polychaetes, and their relation to the coldwater coasts of the southern continents. During this investigation an epizoite on small bivalves was noted, which was identified as the hydrozoan *Monobrachium parasitum* Mereschkowsky, 1877.

Symbiosis, commensalism or parasitism has been seldom described from antarctic waters, but recently this was done by Svoboda et al. (1995, 1997) for hydrozoans and brittle stars. Since *Monobrachium* was very common at some stations and missing from others, one of the aims of our study was to detect the most important factors influencing the settlement and distribution of this hydroid.

A review of symbiotic associations of Cnidaria with Mollusca was given by Rees (1967). He mentioned associations of *Monobrachium parasitum* with bivalves in the Arctic. Since we found associations of hydroids of the genus *Monobrachium* and molluscs in the Antarctic region the problem of bipolarity can be discussed.

# Material and methods

Investigations of antarctic macrozoobenthos were carried out in the austral summer on board FRV "Walther Herwig" from February to April 1985 (Anonymous,

1986) and RV "Polarstern" during November/December 1984 (Hempel, 1985), and October to December 1987 (Fütterer, 1988). Additional data were collected during a winter cruise in May/June 1986 (Schnack-Schiel, 1987). The positions of the stations investigated are shown in fig.1. The research area included the shelves of the South Orkney Islands (11 stations, 5 with *Monobrachium*), Elephant Island (40 stations, 33 with *Monobrachium*), and the region to the west of the Antarctic Peninsula (36 stations, 25 with *Monobrachium*).

A total of 12 samples was collected with a Reineck grab corer (0.25  $m^2$ ) at seven stations, and 199 samples at 78 stations collected with a Van Veen grab corer (0.1 m<sup>2</sup>). At most stations two replicate samples were taken, but in winter five replicates were collected at four stations. In summer 1987 ten replicates were carried out at six stations for statistical comparison. The sampling depth ranged from 50 to 850 m, most samples being taken between 100 and 400m. During the austral winter cruise and the 1987 austral summer cruise sediment subsamples were taken from the surface whenever possible and frozen. Grain-size and water content was determined at these stations. Grain-size determination was carried out by sieving the samples after freeze drying and analysing the sample according to the Wentworth scale. Water content was determined following the DIN procedure (Deutsche Einheitsverfahren, 1981). For statistical analysis the CSS-1 program package was used. In order to find the determining influence for the infection of the main host *Thyasira bongraini* (Lamy, 1910) by Monobrachium, a multilinear regression analysis was calculated. The various values of X and Y are defined in table 1. In order to find the determining abiotic parameter for the distribution of Thyasira bongraini, the parameter Yt was selected as the dependent variable. In order to compute the most important parameter for the infection rate of Thyasira bongraini by Monobrachium the dependent variable Yi was selected as the number of infected T. bongraini. All other factors were defined to be independent variables. The regression was calculated for the winter (1986) and summer (1987) seasons respectively.

All samples were sieved immediately on board using a 0.5 mm screen mesh-size after the meiofauna was decanted over a 0.3 mm plankton net. The macrobenthos was fixed in 4% borax-buffered formalin seawater solution, and the living meiofauna was

Variables:		Sediment type
Yi	number of infected Thyasira bongraini (N/m <sup>2</sup> ) per grab	
Yt, Xt respectively	total number of Thyasira bongraini	
X1	depth in m	
X2	compound of grain size smaller than 0.031 mm	fine silt
X3	compound of grain size between 0.031 and 0.063 mm	silt
X4	compound of grain size between 0.064 and 0.125 mm	silty sand
X5	compound of grain size between 0.126 and 0.25 mm	fine sand
X6	compound of grain size between 0.251 and 0.5 mm	sand
X7	compound of grain size between 0.501 and 1 mm	coarse sand
X8	compound of grain size more than 1 mm	gravel
X9	water content of the sediment	-

Table 1. The dependent and independent variables defined in the multilinear regression.



Fig. 1. Stations investigated during the Antarctic expeditions with RVs "Walther Herwig" and "Polarstern" in summer (circles) and winter (triangles) seasons.

sorted and preserved separately. All sorting was carried out using a binocular microscope to ensure that small-sized animals were not overlooked. Since the buffered seawater solution decalcified the calcareous groups in few days, as recognized during earlier expeditions, the material from the 1987 cruise was preserved in 70% ethanol after fixing for two days.

The length of *Thyasira bongraini* was measured with a eyepiece micrometer in a stereo microscope; 2789 specimens from the 1987 cruise were measured, 510 of them being infected with *Monobrachium parasitum*. The measured individuals were derived from the stations 74, Hope Bay 2, 129 and 137, each station with up to 10 replicate samples. The positions of the stations are:

Sta 74: 61°06.54'S 55°58.86'W, 138 m depth; Sta. Hope Bay 2: 63°23.27'S 57°00.22'W, 213 m depth; Sta. 129: 62°04.9'S 57°39.0'W, 305 m depth; Sta. 137: 62°14.75'S 58°43. 81'W, 178 m depth.

For identification and morphological as well as life-cycle data living specimens were brought to Hamburg. Initially, on the 08.i.1988, 75 infected bivalves (collected 22.xii.87) with 8 living colonies reached Hamburg and were kept in the laboratory at 3°C for more than six months. The hydroids were fed with *Artemia* nauplii and small nematodes. A second sample, collected 22.xii.91 at 63°00'S 57°84'W (4 specimens) and 27.xii.91 at 62°52'S 56°10'W (40 specimens, 15 infected), during cruise no. 10 of RV Polarstern, was also cultured for more than half a year.

#### Results

### The hydroid

Eight and later 15 bivalves bearing *Monobrachium* colonies were cultured for more than six months. After the death of the host, the colonies decreased and finally died. Five colonies, two male and three female, had one or two gonophores, born on a short pedicel directly on the stolons. The mature male gonophores had no radial canals but some rudimentary tentacles. These reduced medusae, 0.26 mm in length and 0.22 mm in diameter, lay on the bottom and showed occasional contractions. The newly released female medusa had four radial canals 16 very short tentacles and a velum. They were 0.42-0.68 mm. in length and 0.24-0.40 mm in diameter. Typical muscular contractions occured but were rather slow and the medusae were not able to swim actively. One eumedusoid contained eight ovaries. Fertilization and further development was not observed.

While the bivalves were alive the *Monobrachium* colonies grew if fed with *Artemia* and if the voided remains of the meal which stuck to the colony were removed. If not removed, the waste impeded the hydranths in catching prey, and the colony starved and finally died. Fully expanded polyps had a length of 1.2 mm maximum and the single tentacle up to 2.12 mm. The dactylozooids were up to 0.35 mm long including the short pedicel.

In the preserved material examined the hydranth length ranged from 0.54 mm to 0.72 mm, and the diameter from 0.11 to 0.16 mm. There was no constriction above the insertion of the single tentacle. The dactylozooids were situated on both flaps of the bivalve at its dorsal margin along to the anterior end and were 0.10 to 0.18 mm in length with a diameter of 0.06 to 0.08 mm. In the preserved gonophores the sex could

be not determined from outside. Small colonies were situated somewhat dorsal from the posterior end of the bivalve. From this initial colony periderm stolons grew along the dorsal sides of both valves towards the anterior end. They later branched and developed an anastomosing net, with a few machozooids at the margin but without any gastrozooids seen in late stages over the whole bivalve exept a small circle around the hinge.

# Infected bivalve species

Fortyfour bivalve species of 19 families were found in the area (Mühlenhardt-Siegel, 1989). The species infected by *Monobrachium parasitum* were generally the small bivalve species *Cuspidaria tenella* Smith, 1907; *Mysella miniuscula* (Martens & Pfeffer, 1886); *M. charcoti* (Lamy, 1906); *Thyasira bongraini* (Lamy, 1910); *Yoldiella valettei* (Lamy, 1906) and, at only one station, *Thracia meridionalis* Smith, 1885 (fig. 2). The habitus of a well developed colony is shown on *Thyasira bongraini* (fig. 3).

## Density

Among the six species mentioned above, *Thyasira bongraini* and *Yoldiella valettei* had the highest density and temporal persistence in the area (tab. 2) but only *T. bongraini* was significantly infected by the hydroid. This last-named species and its epibiont were therefore analysed in more detail.

Table 2. Presence (in % of stations) of host bivalve species infected and uninfected by *Monobrachium parasitum*. Cruise numbers are: PS06: RV Polarstern, November/December 1984; WH68: FRS Walther Herwig, January to April 1985; PS09: RV Polarstern, May/June 1986; PS12: RV Polarstern October to December 1987. Aust. summer (winter) means austral summer (winter). Ele = Elephant Island; Pen = Antarctic Peninsula; Ork = South Orkney Islands.

Season:	PS 06		Aust. s	ummer		Aust. winter	Aι	ist. sumr PS 12	ner
Species	Ele	Pen	Ork	Ele	Pen	Ele	Pen	Ele	Pen
Thyasira bongraini:									
uninfected	30	100	91	100	100	94	100	100	100
infected	0	80	45	93	54	78	44	75	83
Yoldiella valettei:									
uninfected	30	80	73	93	9	89	33	100	100
infected	0	0	0	0	9	0	0	0	50
Mysella miniuscula:									
uninfected	0	0	18	29	0	55	28	100	33
infected	0	0	0	0	0	5	5	0	17
Mysella charcoti:									
uninfected	33	20	0	21	0	5	0	50	17
infected	33	0	0	0	0	5	0	0	0
Cuspidaria tenella:									
uninfected	0	0	27	29	9	37	0	50	33
infected	0	0	0	0	0	0	0	0	17



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Fig. 2. Bivale species infected by Monobrachium parasitum in the research area; a, Cuspidaria tenella; b, Thracia meridionalis, juvenile; c, Mysella miniuscula; d, Yoldiella valettei; e, Mysella charcoti; f, Thyasira bongraini.



Fig. 3. Preserved colonies of Monobrachium parasitum on partly decalcified Thyasira bongraini.

#### Infection rate

The infection rate of *Thyasira bongraini* with *Monobrachium* in the different regions (tab. 3) seemed to be higher in the Peninsula region (0-50%) than at Elephant Island (0-16%) or the South Orkney Islands shelves (0-23.5%). The differences concerning the infection rates per grab between the geographical regions were tested by Mann-Whitney-U-test (Sachs, 1984) and found not to be significant.

Table 3. Infection rate (in %) of *Thyasira bongraini* with *Monobrachium parasitum*. Cruise numbers are: PS06: RV Polarstern, November/December 1984; WH68: FRS Walther Herwig, January to April 1985; PS09: RV Polarstern, May/June 1986; PS12: RV Polarstern October to December 1987. Min. = minimal value; max. = maximal value: med. = median value.

Region	South Orkney		Ele	phant Isl	and	Antarctic Peninsula			
Cruise:	min.	max.	med.	min.	max.	med.	min.	max.	med.
PS 06				0	0	0	0	27.8	2.1
WH 68	0	23.5	0	0	16.3	3.3	0	38.7	2.5
PS 09				0	13.9	3.75	0	6.3	0
PS 12				0	8.2	0	0	50	3.6

# Regional and seasonal differences

Significant regional differences (p < 0.05) (tab. 4) in the infection rate were discovered between the samples of Elephant Island and the Peninsula region in winter (May/June 1986).

There were also significant seasonal differences:

- At Elephant Island between the summer cruises 1985 and 1987 and between winter 1986 and summer 1987. In summer 1987 the infection rate was significantly lower

Table 4. Infection rate per sample, tested with U-test (two-sided test). Significance level p < 0.05. - = no significant difference; + = significant difference; n = too few values; x = decalcified specimens. PS06: RV Polarstern, November/December 1984; WH68: FRS Walther Herwig, January to April 1985; PS09: RV Polarstern, May/June 1986; PS12: RV Polarstern October to December 1987. Ele = Elephant Island; Pen = Antarctic Peninsula; Ork = South Orkney Islands.

		PS 06		WH 68	WH 68		PS 09	PS 09		PS 12	
		Ele	Pen	Ork	Ele	Pen	Ele	Pen	Ele	Pen	
PS 06	Ele		n	n	n	n	n	n	n	n	
	Pen	n		х	-	-		+		-	
WH 68	Ork	n	-		-	-					
WH 68	Ele	n	-			-	-		+		
	Pen	n	-	x	-			+		-	
PS 09	Ele	n			-			+	+		
	Pen	n	+	+		+	+			+	
PS 12	Ele	n			+		+			-	
	Pen	n	-	-		-		÷	-		

than in the other seasons (winter 1986 and summer 1984/85).

--- In the Peninsula region between summer1985 and winter 1986, as well as between winter 1986 and summer 1987, the summer values being higher than the winter ones. Summer values of different years did not differ significantly.

The frequency of infection in the South Orkney Islands samples showed no significant difference from the summer infection rates in the other areas.

# Depth, substratum and abundance effects

A strong relation (correlation coefficient r > 0.7) was found between the mixture of grain sizes smaller than 0.031 mm (variable X2) and the water content of the sediment (variable X9) in both seasons, summer and winter. The stepwise multilinear regression of all parameters mentioned (tab. 1) showed that settlement of *Thyasira bongraini* (Yt) depended:

--- In winter: on a mixture of grain size between 0.064 and 0.25 mm in the sediment:

Yt= 0.632610 X4 - 0.419761 X5

(Rmult.= 0.58, Rsm = 0.34, F = 5.49, degrees of freedom = 3.32).

These sediment parameters accounted for only up to 34% of the settlement of *T*. *bongraini*.

— In summer: on the water content of the sediment, the depth, and the mixture of grain size between 0.031 and 0.063 mm

Yt = 0.675109 X9 - 0.509181 X1 - 0.314645 X3

(Rmult.= 0.47, Rsm = 0.22, F = 3.34, degree of freedom = 6.70).

These sediment parameters accounted for only up to 22% of the density of *T. bon-graini*.

The most important parameters correlating with the infection rate of *M. parasitum* on *T. bongraini* (Yi) were:

- In winter: the density of the host, and the depth

Yi = 0.749766 Xt - 0.402399 X1

(Rmult.= 0.79, Rsm = 0.62, F = 12.67, degree of freedom = 4.31).

These parameters together accounted for up to 62% of the infection of the host.

— In summer: the density of the host, and the grain size between 0.064 and 0.25 mm Yi = 0.662916 X4 + 0.538636 Xt - 0.448548 X5

(Rmult.= 0.71, Rsm = 0.50, F = 7.55, degree of freedom = 9.67).

These parameters account for up to 50% of the infection of the host.

Effect of infection on the growth of the host

The lengths of well calcified specimens of *Thyasira bongraini* obtained in summer 1987 were measured. A difference between uninfected and infected shells was obvious (fig. 4) at each station (p< 0.001, Kolmogoroff-Smirnoff-test; Sachs, 1984), the infected shells being significantly smaller than the uninfected.

# Discussion

Robins, (1972: 80) considered that the diagnostic features separating the three species in the genus Monobrachium (M. parasitum, Mereschkowsky, 1877; M. drachi,



Fig. 4. Length-frequency diagram of *Thyasira bongraini* infected (bars) and not infected (dots) with *Monobrachium parasitum*.

Marche-Marchad, 1963; and *M. antarcticum*, Robins, 1972) were the length of hydranth, the form of the stolons as a reticulum or a mat, the presence or absence of dactylozooids, and the presence of fixed gonophores or free medusae. In table 5 are added the characters found in our material and the data of Kubota (1991). There seems no doubt that *M. drachi* is a valid species, with its up to 2 mm high hydranths raising from a mat, and without dactylozooids on the stolonal reticulum covering the shell valves of the host. Moreover, the free-living but benthic medusae are unique in the genus in developing only four tentacles, even when mature. Up to twelve gonophores have been recorded on one colony. After examination of the type material we also accept *M. antarcticum* to be a valid species because of the mat-like hydrorhiza lacking both periderm-covered stolons and dactylozooids.

Marche-Marchad (1975: 571) summarized differences between the descriptions of *Monobrachium parasitum* of the authors Wagner (1890), Mereschkowsky (1877), Naumov (1957), Fraser (1944), and Hand (1957). The hydranth is described as having hollow or solid tentacles. Since there are papers (e.g. Hand, 1957; Kubota, 1991) which do not mention this character, we cannot decide wether our material with hollow tentacles is representative of the species. Further, a point of constriction has been noted just above the tentacle insertion in at least one population (Naumov, 1969: 547). Neither Mereschkowsky (1877) nor Hand (1957) observed it, and Fraser (1918: 131) pointed out that there is no such insertion like the neck of *Proboscidactyla*. In our material, living or preserved, we did not see such a constriction.

The formation of stolons in some cases is used as a diagnostic character, as in the family Hydractiniidae. However, it might depend on the substrate, as in Clava (see Edwards & Harvey, 1975: 884). Since species of Monobrachium always grow on bivalves, the shape of the hydrorhiza and the colony form, combined with the presence of different zooids, are good separating characters within this genus. But even after separation of the distinctive species M. drachi and M. antarcticum from the remaining collections (all described as M. parasitum), there is no uniform picture in characters of the hydrorhiza, presence or absence of dactylozoids, height of hydranths, and attached or free medusae. Nevertheless, if we consider different states of preservation and take into account the variability of the relevant characters we follow Hand (1957: 86) in his opinion that it might be possible that the Pacific population of Monobrachium represents another species. Our hydroids from Antarctica can also be referred to the M. parasitum group and resemble more those of North Pacific waters than those from the Arctic Ocean and the North Atlantic. Kubota (1991: 3) even supposed *M. parasitum* to be differentiated into three local forms. Only by longterm rearing to elucidate the whole life-cycles of the different populations under similar conditions we might succeed in solving the problems of species identification in this genus.

Associations between Cnidaria and Mollusca are numerous and a brief survey was given by W. J. Rees (1967). Different terms have been used to describe these associations, including symbiosis, parasitism, and commensalism. Commensalism was defined by Nicol (1960) as 'an external relationship between two species which live together in some degree of harmony' whereas Van Beneden (1869) characterised it just as "a company at table". A definition of types of symbioses is given by Cheng (1967). Under symbiosis he summarises parasitism, mutualism, commensalism, and phoresis.

Table 5. Data on distribution, hosts and morphology of the known species of *Monobrachium* after Robins, 1972: 80 (R) with additions after Broch, 1916 (B); Campbell, 1967 (C); Fraser, 1918 (F); Hand, 1957 (H); Kubota, 1991 (K); Levinsen, 1893 (L); Marche-Marchad, 1963, 1975 (M-M); Mereschkovsky, 1877 (M); Naumov, 1957, 1969 (N); Petersen, 1984 (P) and this study (J & M-S).

	M. parasitum	M. parasitum	M. parasitum	M. antartica	M. drachi
Population	Arctic, North Atlantic	Antarctic	Pacific	Antarctica	Tropical East Atlantic
Localities (author)	White Sea (M)	South Orkneys (J& M-S)	Canada, Ppacific (F)	off Signy Island (R)	Senegal, off Gorée (M-M)
	Barents Sea (N)	Elephant Island (J& M-S)	California (H)		
	Chukchi Sea (N)	West of Antarctic Peninsula (J& M-S)	Sea of Japan (N)		
	Sea of Okhotsk (N)		South part Sea of Okhotsk (K)		
	Spitsbergen (B) West Greenland (L, P) Canada, Atlantic (F)		Vancouver Island (0	C)	
Depth range	5-155 m	50-552 m	18-307 m	4-100 m	18 m
Bivalve host	Macoma baltica M. calcarea M. moesta M.tenera Astarte crenata	Thyasira bongraini Cuspidaria tenella Mysella miniuscula M. charcoti Thracia meridionalis Yoldiella valettei	Tellina lata T. solidula T. calcarea Axinopsis viridis A. serricatus Aligena redondoensis Macoma baltica inconspicua Cadella lubrica	Mysella miniuscula M. charcoti Nucula ? falklandica Thyasira spec.	Cuna gambiense
Stolon	reticulum or mat	reticulum	reticulum or mat without periderm	mat	reticulum + mat
Height of hydranth	up to 3 mm	up to 1.2 mm	up to 1 mm	about 1 mm	up to 2 mm
Tentacle	hollow or solid	hollow			solid
Dactylo- zooids	present or absent	present	present	absent	absent
Number of gonophores	up to 6 (R) or 5 to 10 (P)	1 - 2	1 - 2 (R) or up to 4 (F)	up to 6	up to 12
Gonophores	attached eumedusoids	free benthic eumedusoids with 16 tentacles	free medusae or attached eumedusoids with 16 tentacles	probably attached eumedusoids	free benthic eumedusoids with four tentacles

In most associations between hydroids and bivalves, the latter are just used as a hard substrate. Obligate substrate choice of species is rare, at most being typical preference. But there are also specialists like the hydroid of Neoturris pileata (Forskål, 1775) which lives mostly on the shells of the bivalve genus Nucula (cf. Edwards, 1965), or Microhydrula limopsicola Jarms & Tiemann, 1996, from Antarctica up to now observed only on Limopsis hirtella Rochebrune & Mabille, 1889. In Monobrachium parasitum we also found a diagnostic choice of hosts. Only six out of the 44 bivalve species found in the research area (Mühlenhardt-Siegel, 1989) were infected by this hydroid, all six being small burrowing species with a thin periostracum. Robins (1972: 79), too, stated a host specifity especially for the genus Mysella, in which only two species, M. charcoti (Lamy, 1906) and M. minuscula (Martens & Pfeffer, 1886), serve as hosts for Monobrachium antarcticum, whereas another species living in the same locality was never infected. Though the nearest of our stations was only 13 km from the stations of Robins, the same two Mysella species were here infected by M. parasitum. We found difficulty in separating *M. antarcticum* and *M. parasitum* environmentally. There was a zone between 50 and 100 m water depth in which both occurred.

A major factor influencing the infection rate is the density of potential hosts. We investigated the density of the frequently infected bivalve species. We concluded that the density of the host *Thyasira bongraini* could only partly (22-34%) be explained by the chosen substratum. More important environmental factors influencing the settlement and density of the bivalve host may be biotic ones, e.g. the density of other animals or differing productivity of the water column during the seasons. There seemed a limit of 120 bivalves per m<sup>2</sup> below which there was no infection with *M. parasitum*.

Our results also seem to indicate that water depth is important, because we did not find any infected hosts below 532 m, though we collected them at stations as deep as 850 m.

In conclusion the infection rate with *Monobrachium parasitum* in our research area is correlated with host density, depth, and substratum. These three parameters accounted for up to 62% of the infection rate. Another factor correlating with the rate of infection with *M. parasitum* may be the density of prey, such as nematodes and other meiobenthic fauna.

Robins (1972: 81) considered that *Monobrachium antarcticum* did not affect the length of the host's shell. But this statement is restricted in application by his finding that if there are no hydroids, there are other epizoites such as bryozoans and vorticellid protozoans. In our material we hardly ever found epizoites other than *M. parasitum*. Figure 4 shows that infected shells were significantly smaller than uninfected. Since we never found bigger specimens of *Thyasira bongraini* with even residual colonies of the hydroid, the growth of the bivalve may be affected by *Monobrachium*. The explanation may be that the presence of the hydroid increases the drag on the bivalve as it moves through the substrate. That means, more energy is needed to move the same distance. On the other hand these bivalves need movement to have sufficient food supply. So, without beeing parasitic, as suggested by Petersen (1984), the hydroid symbiont may be harmful to its host. In the sense of Cheng (1967: 5-8) the association of *M. parasitum* with bivalves can be classified as symbiosis in the sense of obligatory commensalism.

#### **Bipolarity**

According to Crame (1974: 205) there are three main models of evolution of polar biotas:

1. The majority of plant and animal taxa originated from tropical/subtropical regions. In time some of them were displaced to higher latitudes where they became relicts.

2. A number of major taxa arose in the polar regions, in time some of these moving into lower latitudes.

3. In the past there were widespread taxa ranging from one polar region to the other, their ranges of distribution later being disrupted in the equatorial region by a topographic and/or climatic barrier.

Stepanjants et al. (1997: 456) listed seven more or less different theories to explain bipolarity, and extended the phenomenon by the term 'binomic bipolarity'. They (1997: 462) concluded that bipolar distribution in Hydrozoa is largely a result of present-day migration from the northern to the southern hemisphere. According to Van der Spoel (1991: 495) the recent northern higher-latitude Leptolida may have developed from a pre-Cretaceous arctic stock, but more likely from an antarctic development centre. Subsequent migration to the north during periods of intense cooling gave rise to the northern populations.

We cannot be sure how Monobrachium parasitum developed its present bipolarity, but we prefer to follow van der Spoel. His hypothesis proposes that dispersal of species after the Mesozoic-Cenozoic extinction period must have emanated from two central areas, the Indo-Malayan Region and the Antarctic (van der Spoel 1991: 492). Since there are two closely related but highly specialized species of *Monobrachium* in the Antarctic, sometimes inhabiting the same hosts (Mysella charcoti, M. minuscula) in localities not more than 13 km away from each other, we assume that both species originate from that region. During the supposed cooling Monobrachium could have moved north and its distribution extend from pole to pole. After warming again, M. drachi might have developed its specific features, especially its distinctive medusa, under the different ecological factors of the tropics. This model can also serve to explain the differences between populations of *M. parasitum* in the northern hemisphere documented by the descriptions of several authors [Mereschkowsky, 1877; Broch, 1916; Naumov, 1969 (North Atlantic); Fraser, 1918; Hand, 1957; Campbell, 1967; Kubota, 1991 (North Pacific)]. The sometimes minute differences in the characters listed above have not (yet) led to different species being recognised but already Robins (1972: 80) listed the Arctic/North Atlantic population separately from the Pacific population. Research with molecular methods is needed to learn more about speciation in the genus Monobrachium.

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