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

G. Jarms & U. Mühlenhardt-Siegel


Key words: hydroids; Monobrachium; bivalves; symbiosis; ecology; bipolarity.

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 cold-water 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 m²) at seven stations, and 199 samples at 78 stations collected with a Van Veen grab corer (0.1 m²). 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 400 m. 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

<table>
<thead>
<tr>
<th>Variables:</th>
<th>Sediment type</th>
</tr>
</thead>
<tbody>
<tr>
<td>Yi</td>
<td>number of infected <em>Thyasira bongraini</em> (N/m²) per grab</td>
</tr>
<tr>
<td>Yt, X respectively</td>
<td>total number of <em>Thyasira bongraini</em></td>
</tr>
<tr>
<td>X1</td>
<td>depth in m</td>
</tr>
<tr>
<td>X2</td>
<td>compound of grain size smaller than 0.031 mm</td>
</tr>
<tr>
<td>X3</td>
<td>compound of grain size between 0.031 and 0.063 mm</td>
</tr>
<tr>
<td>X4</td>
<td>compound of grain size between 0.064 and 0.125 mm</td>
</tr>
<tr>
<td>X5</td>
<td>compound of grain size between 0.126 and 0.25 mm</td>
</tr>
<tr>
<td>X6</td>
<td>compound of grain size between 0.251 and 0.5 mm</td>
</tr>
<tr>
<td>X7</td>
<td>compound of grain size between 0.501 and 1 mm</td>
</tr>
<tr>
<td>X8</td>
<td>compound of grain size more than 1 mm</td>
</tr>
<tr>
<td>X9</td>
<td>water content of the sediment</td>
</tr>
</tbody>
</table>

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 an 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 08.1.1988, 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 occurred 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 except 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. bong-


<table>
<thead>
<tr>
<th>Species</th>
<th>PS 06</th>
<th>PS 09</th>
<th>PS 12</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ele</td>
<td>Pen</td>
<td>Ele</td>
</tr>
<tr>
<td>Thyasira bongraini:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>uninfected</td>
<td>30</td>
<td>100</td>
<td>91</td>
</tr>
<tr>
<td>infected</td>
<td>0</td>
<td>80</td>
<td>45</td>
</tr>
<tr>
<td>Yoldiella valettei:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>uninfected</td>
<td>30</td>
<td>80</td>
<td>73</td>
</tr>
<tr>
<td>infected</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mysella miniuscula:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>uninfected</td>
<td>0</td>
<td>0</td>
<td>18</td>
</tr>
<tr>
<td>infected</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Mysella charcoti:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>uninfected</td>
<td>33</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>infected</td>
<td>33</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>Cuspidaria tenella:</td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>uninfected</td>
<td>0</td>
<td>0</td>
<td>27</td>
</tr>
<tr>
<td>infected</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
</tbody>
</table>
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.
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.

<table>
<thead>
<tr>
<th>Region</th>
<th>South Orkney</th>
<th>Elephant Island</th>
<th>Antarctic Peninsula</th>
</tr>
</thead>
<tbody>
<tr>
<td>Cruise:</td>
<td>min.</td>
<td>max.</td>
<td>med.</td>
</tr>
<tr>
<td>PS 06</td>
<td>0</td>
<td>0</td>
<td>0</td>
</tr>
<tr>
<td>WH 68</td>
<td>0</td>
<td>23.5</td>
<td>0</td>
</tr>
<tr>
<td>PS 09</td>
<td>0</td>
<td>13.9</td>
<td>3.75</td>
</tr>
<tr>
<td>PS 12</td>
<td>0</td>
<td>8.2</td>
<td>0</td>
</tr>
</tbody>
</table>

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.

<table>
<thead>
<tr>
<th></th>
<th>PS 06</th>
<th>WH 68</th>
<th>WH 68</th>
<th>PS 09</th>
<th>PS 12</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Ele</td>
<td>Pen</td>
<td>Ork</td>
<td>Ele</td>
<td>Pen</td>
</tr>
<tr>
<td>PS 06</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ele</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
<td>n</td>
</tr>
<tr>
<td>Pen</td>
<td>n</td>
<td>x</td>
<td>-</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>WH 68</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ork</td>
<td>n</td>
<td>-</td>
<td>-</td>
<td>-</td>
<td></td>
</tr>
<tr>
<td>WH 68</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ele</td>
<td>n</td>
<td>-</td>
<td>x</td>
<td>-</td>
<td>+</td>
</tr>
<tr>
<td>Pen</td>
<td>n</td>
<td>+</td>
<td>+</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>PS 09</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ele</td>
<td>n</td>
<td>+</td>
<td>-</td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Pen</td>
<td>n</td>
<td>-</td>
<td>-</td>
<td>+</td>
<td>+</td>
</tr>
<tr>
<td>PS 12</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td>Ele</td>
<td>n</td>
<td></td>
<td></td>
<td>+</td>
<td></td>
</tr>
<tr>
<td>Pen</td>
<td>n</td>
<td></td>
<td></td>
<td>-</td>
<td></td>
</tr>
</tbody>
</table>

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

— In the Peninsula region between summer 1985 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:

\[ Y_t = 0.632610 X_4 - 0.419761 X_5 \]

(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

\[ Y_t = 0.675109 X_9 - 0.509181 X_1 - 0.314645 X_3 \]

(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. bongraini*.

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
\[ Y_i = 0.749766 X_t - 0.402399 X_1 \]
(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
\[ Y_i = 0.662916 X_4 + 0.538636 X_t - 0.448548 X_5 \]
(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*, *M. 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 whether 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 dactylozooids, 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 long-term 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).

<table>
<thead>
<tr>
<th>Species</th>
<th>Population</th>
<th>Localities</th>
<th>Depth range</th>
<th>Bivalve host</th>
<th>Stolon</th>
<th>Height of hydranth</th>
<th>Tentacle</th>
<th>Dactylozooids</th>
<th>Number of gonophores</th>
<th>Gonophores</th>
</tr>
</thead>
<tbody>
<tr>
<td><em>M. parasitum</em></td>
<td>Arctic, North Atlantic</td>
<td>White Sea (M)</td>
<td>5-155 m</td>
<td><em>Macoma baltica</em></td>
<td>reticulum</td>
<td>up to 3 mm</td>
<td>hollow</td>
<td>present or absent</td>
<td>up to 6 (R) or 5 to 10 (P)</td>
<td>attached</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Barents Sea (N)</td>
<td>50-552 m</td>
<td><em>M. calcarea</em></td>
<td>reticulum</td>
<td>up to 1.2 mm</td>
<td>solid</td>
<td>present</td>
<td>1 - 2</td>
<td>eumedusoids</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Chukchi Sea (N)</td>
<td>18-307 m</td>
<td><em>M. moesta</em></td>
<td>reticulum</td>
<td>up to 1 mm</td>
<td>hollow</td>
<td>present</td>
<td>1 - 2 (R) or up to 4 (F)</td>
<td>free benthic</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sea of Okhotsk (N)</td>
<td>4-100 m</td>
<td><em>M. tenera</em></td>
<td>reticulum</td>
<td>about 1 mm</td>
<td>solid</td>
<td>present</td>
<td>up to 6</td>
<td>eumedusoids</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Spitsbergen (B)</td>
<td>18 m</td>
<td><em>Astarte crenata</em></td>
<td>reticulum + mat</td>
<td>up to 2 mm</td>
<td>solid</td>
<td>absent</td>
<td>up to 12</td>
<td>free benthic</td>
</tr>
<tr>
<td></td>
<td></td>
<td>West Greenland (L, P)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>eumedusoids</td>
</tr>
<tr>
<td></td>
<td></td>
<td>Canada, Atlantic (F)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td>with four tentacles</td>
</tr>
<tr>
<td><em>M. antarctica</em></td>
<td>Antarctic</td>
<td>South Orkneys</td>
<td>5-155 m</td>
<td><em>Thyasira bongraini</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Elephant Island</td>
<td>50-552 m</td>
<td><em>Cuspidaria tenella</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td><em>M. drachi</em></td>
<td>Pacific</td>
<td>Canada, Pacific</td>
<td>18-307 m</td>
<td><em>M. miniuscula</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>California</td>
<td>4-100 m</td>
<td><em>T. calcarea</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Sea of Japan</td>
<td>18 m</td>
<td><em>A. serricatus</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>South part Sea of Okhotsk</td>
<td></td>
<td><em>Aligena redondoensis</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Vancouver Island</td>
<td></td>
<td><em>Macoma baltica</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Senegalese</td>
<td></td>
<td><em>Astarte crenata</em></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
<tr>
<td></td>
<td></td>
<td>Gorée (M-M)</td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
<td></td>
</tr>
</tbody>
</table>

**Notes:**
- *Thyasira bongraini* and *Cuspidaria tenella* are the symbiotic hosts for *Monobrachium* species.
- *M. moesta* and *M. tenera* are known to have a similar distribution range.
- *M. drachi* is known to have a wider distribution range compared to the other species mentioned.
- The table includes references to previous studies for each species, indicating the sources of the data.
- The distribution range and localities are provided for each species.
- The table also includes additional information on population distribution, host species, and morphological characteristics.
- The table highlights the importance of understanding the distribution and morphology of these species for further research and conservation efforts.

**References:**
- Robins, 1972: 80
- Broch, 1916
- Campbell, 1967
- Fraser, 1918
- Hand, 1957
- Kubota, 1991
- Levinsen, 1893
- Marche-Marchad, 1963, 1975
- Mereschkovsky, 1877
- Naumov, 1957, 1969
- Petersen, 1984
- Jarms & Mühlenhardt-Siegel.
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 specificity 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 m² 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 meiofaunal 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 being 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.

Acknowledgements

We are indebted to Prof. em. Dr G. Hartmann who gave us the chance to participate in the project funded by the Deutsche Forschungs Gemeinschaft under No. Ha 138/34.
References


Campbell, R.D., 1967. *Monobrachium parasitum*, a one tentacled hydroid, collected at Vancouver
Island.— Pac. Sei. 21(3): 431.

Cheng, T.C, 1967. Marine molluscs as hosts for

Concerns.— Springer Verlag: 188-214.

Deutsche Einheitsverfahren zur Wasser- Abwasser- und Schlammuntersuchung. — (Hrsg. von der


Fraser, C. M., 1918. *Monobrachium parasitum* and other West Coast hydroids.— Trans. Roy. Soc. Cana-
da (3) 12 (Sec. IV): 131-138.

Hartmann, G. 1986. Antarktische benthische Ostracoden I (Mit einer Tabelle der bislang aus der
Antarktis bekannten Ostracoden). Auswertung der Fahrten der „Polarstern“ Ant II/2 und der

Hartmann, G. 1987. Antarktische benthische Ostracoden II. Auswertung der Fahrten der „Polarstern“
Ant II/2 und der Reise 68/1 und 2 der „Walther Herwig“ 2. Teil: Elephant Island und Bransfield
Straße.— Mitt. hamb. zool. Mus. Inst. 84: 115-156.

Hartmann, G. 1988. Antarktische benthische Ostracoden III. Auswertung der Reise des FFS „Walther


sp., epibiotic on bivalve shells from the antarctic.— Scientia Marina 60 (1): 109-115.

Kubota, S., 1991. An undescribed colony form of *Monobrachium parasitum* (Limnomedusae: Olindiasi-

Levinsen, G. M. R., 1893. Meduser, Ctenophor og Hydroider fra Grønlands Vestkyst, tiligmed

Marche-Marchad, I., 1963. Un nouvelle hydraire à méduse non pelagique *Monobrachium drachi* n.sp.

Marche-Marchad, I., 1975. Observations sur *Monobrachium drachi* Marche-Marchad Hydraire (Lim-
nomedusae) a méduse non pelagique commensal d’un lamellibranche de la côte occidentale

Merenschkowsky, M. C. 1877. On a new genus of hydroids from the White Sea, with a short descrip-