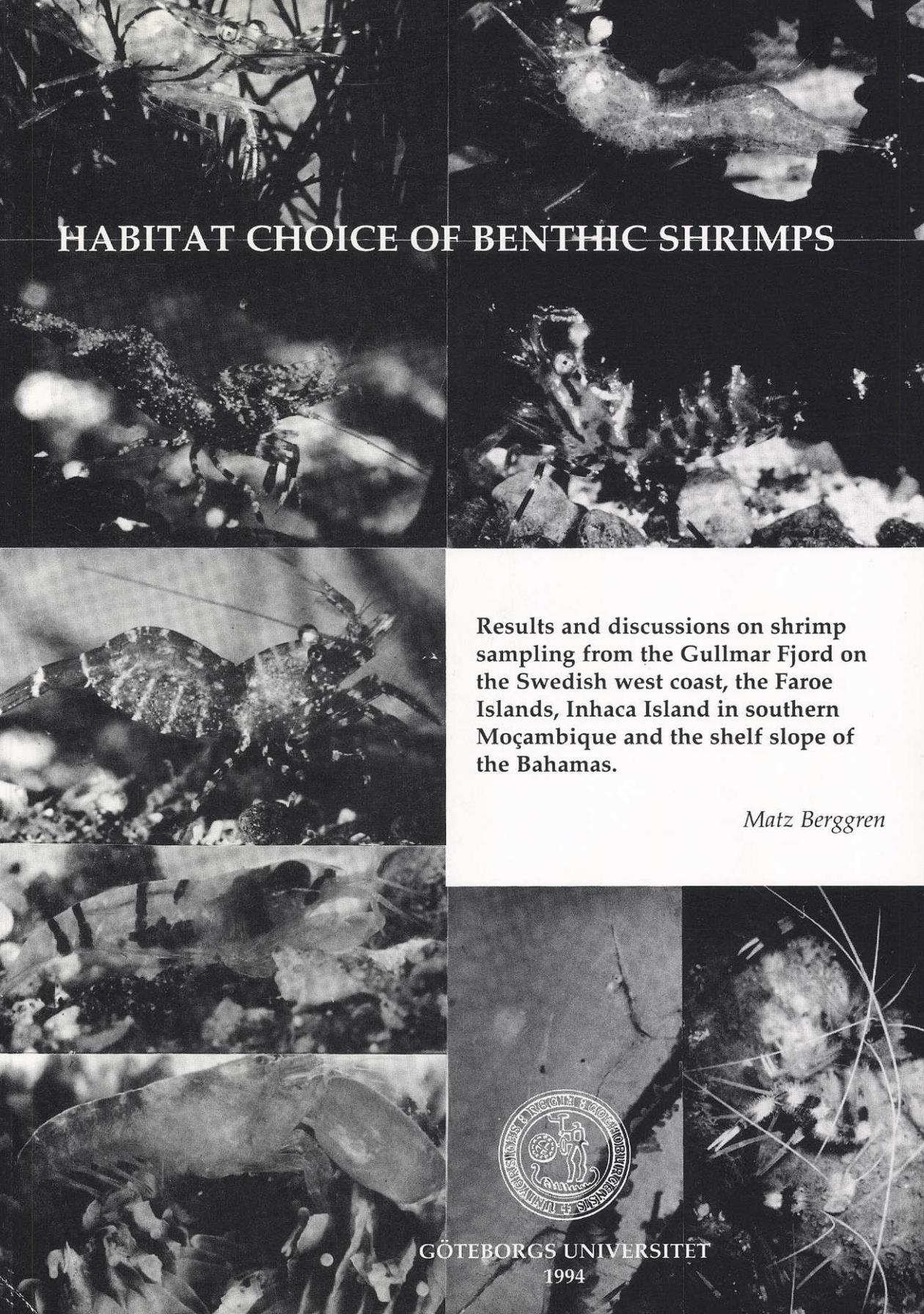




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# HABITAT CHOICE OF BENTHIC SHRIMPS

Results and discussions on shrimp sampling from the Gullmar Fjord on the Swedish west coast, the Faroe Islands, Inhaca Island in southern Moçambique and the shelf slope of the Bahamas.

*Matz Berggren*



GÖTEBORGS UNIVERSITET  
1994



Göteborg University  
Faculty of Natural Sciences

## **HABITAT CHOICE OF BENTHIC SHRIMPS**

**Results and discussions on shrimp sampling from the Gullmar Fjord on the Swedish west coast, the Faroe Islands, Inhaca Island in southern Moçambique and the shelf slope of the Bahamas.**

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Dissertation

Marine Zoology  
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*Key words:* Benthic shrimps, habitat choice, behaviour, associations, distribution, speciation, sibling species.

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ABSTRACT: Field investigations on the shallow-water shrimps of the Gullmar Fjord area, Swedish west coast and various coastal localities of the Faroe Islands have been made by selective sampling among different algal habitats using SCUBA-diving. The different species of shallow-water shrimp in the algal zone are found to utilize different algal species/communities as habitat. The shrimps found among algae do not normally migrate seasonally in contrast to those living on sand, mud or *Zostera*. The selectivity towards a special dominating algal habitat in these shrimps is higher at the Faroes than in the Gullmar Fjord area. The present shallow-water shrimp fauna at the Faroe Islands has little connections to the European mainland and the British Isles due to the North-East Atlantic current. The larvae suppling the Faroes probably come from Iceland.

The tropical part of this work has been done at Inhaca Island, Moçambique. The area is shown to be tropical according to the shrimp fauna found, situated at a subtropical latitude. The addition of new shrimp species for Moçambique from the Inhaca area accounts for 39 % of the shrimp species. The number of shrimps found to be associated with other invertebrate species at Inhaca are 50 %. The area has a complex habitat structure, thereby maintaining a diverse shrimp fauna. A locality situated at the same latitude, Shark Bay on the east Australian coast, show a much lower number in both the species and number of associates in the shrimp fauna. The term commensalism often used for associations have been found inappropriate and a more generalized term, *colalism*, is proposed.

A few examples of shrimp associations from deep-sea localities at the Bahamas are given. These investigations implies that associated shrimp species in the deep-sea are expected to be common.

The implications of a strict habitat choice, especially the associated shrimps in the tropics, in the speciation process are discussed. The gist of the discussion is that some families, subfamilies or genera have been very successful in radiating in the complex environments of the tropics. The result of that strategy is a high degree of speciation and thereby lowering the intraspecific competition for a limited host supply.

*"If One Does Not Know The Names,  
Ones Knowledge Of Things Is Useless"*

Isidorus of Sevilla, 560 - 636. Archbishop of Sevilla and a Saint.

### Aim of this study

This work started as a part-time study with habitat related sampling of the shrimps in the algal zone outside the Kristineberg Marine Research Station from 1981 to 1986. The objectives were to study the habitat choice, migrations (both seasonal and day and night), food selection and different aspects in behaviour. However, in 1986 I started to participate in a co-operative project between the Royal Swedish Academy of Sciences (through the former Kristineberg Marine Biological Station) and the Universidade Eduardo Mondlane, Maputo, Moçambique. This programme was administrated by the Swedish foreign-aid organization for research, SAREC. It was through this project I came in contact with the tropical shallow water shrimp fauna. The wide variety of different solutions to avoid predators and obtain a steady food source was fascinating. This gave raise to questions around habitat choice and speciation in both the tropical and the temperate environment. The different areas to investigate grow larger when I got the possibility to perform studies on the shrimps at the Faroe Islands and received deep-sea material collected by the Johnson Sea Link from the Bahamas. This made it possible to focus my research on geographical comparison of the different habitat strategies for shrimps .

Starting with a thought of making an ecological study of the shallow-water shrimps from the west coast of Sweden I ended up standing with one foot in ecology (habitats) and one in taxonomy (tropical species).

This arises the question concerning the focus of this thesis. The aim was to ascertain different aspects of habitat choice and discuss the implications in the speciation process. One question was if the shallow-water shrimps in the algal zone in northern waters choose their habitat to species, group or any algae? Are they behaving differently between the variable (concerning salinity and temperature) Swedish west coast and the less variable Faroe Islands? Another question is if the extreme habitat specialists ("associates") only can be found in "true" tropical waters? The last question was if associated shrimps occurs on the continental slopes and with which host species they are found?

THIS THESIS IS A SUMMARY OF THE FOLLOWING ARTICLES AND  
MANUSCRIPTS, REFERRED TO BY THEIR ROMAN  
NUMERALS:

- I. Berggren M., and Svane I. 1989. *Periclimenes ingressicolumbi*, new species, a pontoniine shrimp associated with deep-water echinoids off San Salvadore Island in the Bahamas, and a comparison with *Periclimenes milleri*. **J. Crust. Biol.** 9(3):432-444.
- II. Berggren M. 1990. *Dasella herdmaniae* (Lebour), (Decapoda, Natantia: Pontoniinae), from Moçambique and establishing of the new species *D. brucei*. **J. Crust. Biol.** 10(3):554-559.
- III. Berggren M. 1990. Occurrence of the fascigera forms of *Hippolyte varians* (Leach.) in the Gullmarsfjord, Sweden, with comparisons from the Faroe Islands. **Cahiers de Biologie Marine**: 31: 147-157.
- IV. Berggren M. 1991. *Athanopsis rubicinctuta*, new species (Decapoda, Natantia: Alpheidae), a shrimp associated with an echiuroid at Inhaca island, Moçambique. **J. Crust. Biol.** 11(1):166-178.
- V. Berggren M. 1993. Using the composition of the littoral shrimps of Inhâca Island, Mozambique, as evidence of climate conditions. In: **Workshop on tropical coastal lagoon ecosystems, Inhâca Island, Mozambique, December 3-5, 1991. SAREC Documentation, Conference Reports. 1993:1 :202-207.**
- VI. Berggren M. 1993. Aquarium experiments on habitat choice of littoral shrimps of the Faroe Islands. **Crustaceana** 65:129-143.
- VII. Berggren M. 1993. *Spongiocaris hexactinellicola*, a new species of stenopodidean shrimp (Crustacea: Decapoda: Stenopodidae) associated with hexactinellid sponges from Tartar Bank, Bahamas. **J. Crust. Biol.** 13(4) 784:792.
- VIII. Berggren, M. 1994. *Periclimenes nomadophila* and *Tuleariocaris sarec*, two new species of pontoniine shrimps (Crustacea: Decapoda: Pontoniinae), from Inhaca Island, Moçambique. **J. Crust. Biol.** (in press).
- IX. Berggren, M. 1994. The shallow water shrimps of the Faroe Islands. (in ms, ready to be submitted).
- X. Berggren, M. 1994. The shrimps of the algal zone in the Gullmar Fjord area, west coast of Sweden. (in ms, ready to be submitted).

## INTRODUCTION

Habitat choice among animals, marine as well as limnic and terrestrial, is mostly a combination of predator avoidance, food availability, living space, habitat accessibility and competition success. Since the benthic or semi-benthic shallow-water shrimps normally are rather omnivorous, predator avoidance is probably one of the major structuring forces in selecting their habitat preferences. Considerable effort has been made to try to explain different behaviour and adaptation to the habitat for different species of shrimps, especially in tropical seagrass meadows. However, this is not the case with shrimps in the algal zone in the northern seas (temperate/subarctic zone). The habitat reference in literature for these shrimps is still "living amongst algae".

To be protected from predators (most commonly fishes) actively searching for food, the prey has to become "invisible", because these predators are using sight to find and recognize their prey. To avoid being recognized and fitted into the prey image of a predator, the shrimp has to adapt to and utilize a special habitat. This will ensure that the survival will be greater in the selected habitat than in any other habitat. This use of a habitat as a refuge in a dangerous environment enhances different modifications of the shrimp towards the habitat in the evolutionary processes. These modifications can be in coloration, morphology, physiology or behaviour, as single or combined effects. In studies of shrimps (*Hippolyte coerulescens* (Fabricius) and *Latreutes fucorum* (Fabricius)) associated with pelagic *Sargassum* (mostly *S. natans* (L.)), Hacker and Madin (1991) found that small or slender shrimps mimic habitat substructures while the large ones use camouflage. "Habitat mimicry" means an organism resembling in size, shape, colour and behaviour a particular component of a chosen habitat to avoid being recognized as a prey. "Habitat camouflage" is an organism resembling in colour pattern the surrounding habitat so that a predator can not perceive it against the background (Hacker and Madin 1991). That the fit between the body-size and habitat architecture is important in hiding from predators has been shown by Hacker and Steneck (1990) also for amphipods among benthic algae. These two main strategies can of course in some species of shrimps appear as a shift from mimicry towards camouflage as an individual grows larger (Hacker and Madin

1991). The colour adaptation in tropical shrimps can be divided into two major groups according to Bruce (1976): 1. Pattern blending with the background (cryptic-, disruptive- and transparent patterns) and 2. Pattern contrasting with the background ("irrelevant"- or signal patterns and nocturnal colour changes).

The large, more richly coloured shrimps are very obvious when removed from their habitat, but sometimes are so even in their habitat. This can be explained by the effect the colour and especially the colour pattern (disruptive colour pattern) has on the potential predators. Disruptive coloration is found in many shrimps to avoid being recognized as a prey (Bauer 1981). In those shrimps the colour pattern is well developed with defined patches or lines that for the predator (normally searching for a bilateral symmetry in their prey image) breaks up the animal's form into two or more apparently unconnected parts. This is why some shrimps can be easily seen by humans but not by the predator. However, vision is not only important for the predator but also for the shrimp, both in finding the most suitable habitat and in responding behaviourally the right way when a predator is approaching. Vision stimuli of the habitat pattern within narrow limits (highly contrasting vertical lines => mimicking the sea grass *Zostera marina*) have been shown to attract the shrimp *Hippolyte californiensis* Holmes, which is living in this habitat (Barry 1974). The same has been shown for a pontoniid shrimp, *Tuleariocaris zanzibarica* Bruce, which lives among the spines of the sea urchin *Diadema setosum*. The seagrass dwelling shrimps *Palaemonetes vulgaris* and *Palaemon floridanus*, were shown in a study by Coen *et al.* (1981) to select their micro habitat by form alone. The study showed that the selected habitat also gave the best protection from their normal predators. In a work by Main (1987) on the predation on the shrimp *Tozeuma carolinense* in seagrass meadows, he showed that not only the cryptic coloration is important but also the behavioural responses towards a predator. When a predator approaches the shrimp it moves from the base of the blades to the canopy (*e.g.* microhabitat shift) where the predators have difficulties to search for prey. Also when a predator approach, the shrimp moves around the seagrass blade to hide on the backside (Main 1987). A few examples from Inhaca Island, Moçambique show for instance that the pontoniid shrimp *Zenopontonia norveca* Kemp, hides on the aboral side

of its host (*Pentaceraster mammilatus*) when disturbed and *Alpheus lottini* Guerin retreats backwards among the finger-like branches of the coral *Pocillophora* sp. (authors' observations *in situ*). The shrimps in the algal zone of the Swedish west coast, e.g. *Hippolyte varians* or *Thorulus cranchii*, becomes immobile, relying of their cryptic coloration in the presence of a predator and escaping with "jack-knife"-like movements when the predator is too close and disappearing amongst the surrounding algae. Normally this behaviour takes them between 0.5 - 1 m away, where they again become immobile clinging to another alga of the same type as the previous one (diving observations by the author).

The results from the investigation by Coen *et al.* (1981) show that a structurally complex habitat gives better protection and thereby can be a limiting resource.

Several authors have stated that there is a correlation between habitat complexity and species number (Abele 1976a, Coen *et al.* 1981, Leber 1985, Heck & Wilson 1987). This has been shown, especially in tropical seagrass communities. However, an increase in the seagrass species is not necessarily correlated to an increase in the number of associated invertebrates whereas the biomass, e.g. a dense habitat substratum is normally found to be strongly correlated to species number and abundance of invertebrates found (Heck & Wetstone 1977). The algal zone in the northern hemisphere is a complex habitat with a rather high biomass, and is also more temporally stable and complex than the *Zostera* meadows found at the same latitudes. Among the benthic shallow water shrimp species at those latitudes there are more species to be found amongst algae than in other types of habitats. In respect to the species number and habitat complexity, the northern algal zone has more similarities with tropical seagrass meadows than with the seagrass meadows at the same latitudes. This because the predation pressure, species richness and habitat-complexity increase with decreasing latitudes in the seagrass meadows (Heck & Wilson 1987).

The shrimp species found in the algal zone can be divided into three groups, according to their habitat strategies. The first group only settle and grow to a certain stage before they start to migrate deeper out of the algal zone, the second migrate seasonally in and out of the algal

zone, and the third are residents of the algal zone throughout the year. The last group also includes species that are found in deeper localities without vegetation, but they do not perform migrations between the different localities. In this group of more or less 'permanent' residents of the algal zone it might be expected to find habitat specialists. The habitat specialists in the extreme form are the associated species ("commensals"), mostly found in the tropics. For example, in the Caribbean the number of crustacean and coral species is strongly correlated implying that the dominant species are specialists on a specific part of the habitat (Abele 1976a). Normally space is the limiting resource for the associated crustaceans on coral reefs as shown by Abele (1976b) in two different coral reefs (one stable and one fluctuating environment) of the Pacific coast of Panama. Since most of the associated crustaceans on coral reefs have sessile hosts they are functionally sessile. Habitat specialists (associates) were more common in the stable than in the fluctuating environment. However, although there were fewer habitat specialists in the fluctuating environment there were far more habitat generalists and therefore it became a more species-rich environment (Abele 1976b). This implies that a complex habitat with a large number of associates does not necessarily need to be the most species rich when comparing with a similar habitat but with fewer associated species. According to Vermeij (1983), the two major factors which are important for the evolution of intimate associations and mutualisms seem to be predation and low nutrient availability. He also predicts that such associations are more common in tropical oceans vs. temperate, because of more nutrient-poor conditions in the tropics. Discussions about which is the most important factor to promote these associations, a stable environment or low production areas or both, still occur.

When considering all preceding statements, the following questions are formulated. (1) Do the shallow water shrimps in the north-eastern Atlantic select their habitat according to specific algal species or do they use any type of alga? (2) Can there be any difference in the habitat selectivity of the same species of shrimp, according to its geographical location? In the northern hemisphere this might occur between the Swedish west coast and the Faroe Islands. The Swedish west coast is a variable marine environment with regard to salinity and temperature,

and it is nutrient rich. The Faroe Islands show low variability in these factors on the exposed coasts, but the fjords take a more intermediate position (compared to the Swedish west coast).

Questions concerning the tropical shallow-water shrimps are as follows.

(3) Do the shallow-water shrimps from complex environments in the subtropics (Inhaca Island, southern Moçambique) also show a high degree of association? (4) Is the shallow-water shrimp fauna at Inhaca Island similar to that of the eastern waters of the Indian Ocean at the same latitude, as Shark Bay, in western Australia (Jones 1988)?

(5) Do deep-water shrimps show any associations with other animals? If so, do they show the same types of associations as those in the shallow tropical waters? (6) The final question to discuss is the selection value of associations and their implications in speciation.

## MATERIAL AND METHODS

### Sweden and the Faroe Islands

At the Faroe Islands the shrimps were collected (late August 1987 and early June 1988) at 18 different localities (see Thesis-work IX, Fig. 1), from both high and low exposed localities. On the Swedish west coast they were collected close to the Kristineberg Marine Research Station (see Thesis-work X, Fig. 1) at the mouth of the Gullmar Fjord (occasional sampling from Dec. 1982 to Aug. 1986, with an intense sampling effort during 1984-1985).

All collections were made using a specially designed dip-net during SCUBA-diving, because of the importance of sampling within only one type of habitat (algal species/group) for each individual sample. Sampling during diving was made from about 25 m depth to the shore (algal zone). For sampling details, see Berggren (Thesis-work IX and X).

A Multi Dimensional Scaling (MDS) was performed on the untransformed numerical data of *Hippolyte varians*, *Thorulus cranchii* and *Eualus pusiolus*. The graphical output and calculation were made using the

multivariate programme PRIMER (Plymouth Routines In Multivariate Ecological Research).

### Inhaca Island

From 1986 to 1992, I spent one month per year in Moçambique in a co-operative project administered by SAREC (the Swedish Agency for Research Cooperation with Developing Countries) between the EBM/UEM (Estação Biologia Marítima/Universidade Eduardo Mondlane) and the Kristineberg Marine Biological Station (KMBS)/The Royal Swedish Academy of Sciences. During my visits to Moçambique I sampled at different localities at Inhaca Island to build a species list of the shallow-water shrimps. The main part of the field-work was carried out during 1986 - 1989 with about two weeks of sampling each year. Additional sampling was made in the following three years. The identification of the shrimp material from Inhaca was made at KMBS in Sweden.

Natant crustaceans of Inhaca Island have been collected at different areas and habitat types. The only area not covered is the eastern, open ocean side (Indian Ocean). Habitat selective sampling has so far not been possible there because of the heavy wave exposure. All collected animals were preserved in 5% formaldehyde for at least 24h, thereafter transferred to a solution of 70% alcohol with 5% glycerol. Samples are labelled with date, area, habitat and depth. In cases of association where the host animal is not determined to species it is preserved together with the shrimp.

The different collection methods used in tidal flats, seagrass meadows, and on sandy bottoms down to 1 m were a small man-pulled trawl, dip nets, digging and in very shallow (<0.2 m) tidal flats a Yabby pump (Hailstone and Stephenson, 1961). In waters exceeding 1 m depth or on hard substrata as the coral reefs sampling was done by snorkelling or SCUBA while using delicate picking, enclosing in a net bag (0.7 m long and 0.1 m<sup>2</sup> opening with the diameter = 0.6 m and mesh size 0.5 mm) and dip net. During the sampling careful notes were made on type of habitat where the shrimps were caught.

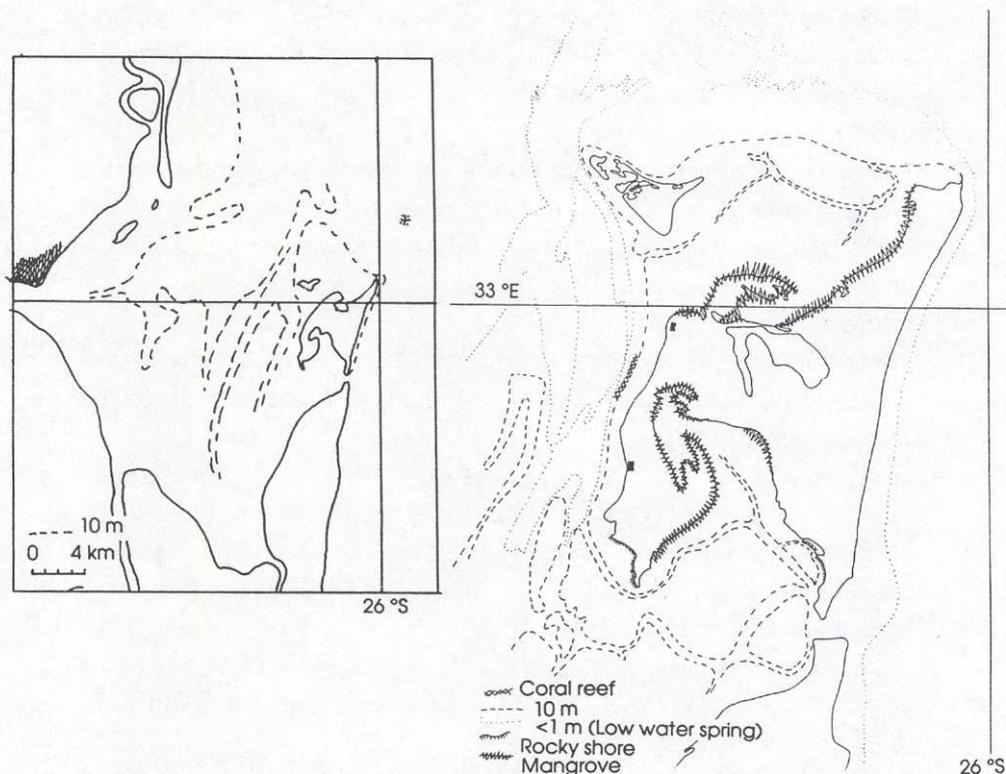


Fig. 1. Left map: Inhaca Island on the outside of the Maputo Bay (Maputo area = hatched area to the left). Right map: Inhaca Island with Ilha dos Portugueses and part of the mainland peninsula (south).

The habitats of Inhaca island where shrimps were collected can be divided into 8 types (Fig. 1):

#### 1. Coral reef

On the coral reefs, sampling was on all three main reefs (*Ilha dos Portugueses*, *Barreria Vermelha* and *Ponta Torres*). The areas are well covered according to dominant species.

#### 2. Cliff wall

The cliff wall at *Ponta Torres* is a special type of habitat at Inhaca with a steep rock wall down to 9-10 m depth.

### 3. Seagrass bed

Apart from bare sand this is the most common habitat on the shallow areas of the western side of Inhaca. Most of the sampling took place outside the station and in the area between Ilha dos Portugeses and Inhaca island (*Banco da Sangal*).

### 4. Mangal area

The major mangrove communities are located along the south-western side of the island and sampling have been made in the outlet at *Ponta Raza* and the inner south-western parts of the *Saco* area.

### 5. Tidal flats

These are the main habitats of western Inhaca between the seagrass beds and the shoreline and sampling has mainly taken place in the area outside the station.

### 6. Rock outcrop

The only true rocky shore with tidal pools is located at the northern end of Inhaca, *Cabo Inhaca*. Sampling was mainly done in the tidal pools of that area.

### 7. Deeper areas (about 15 m)

Diving has been done in the *Inhaca channel* (sand) and on the rocky area called *Baixo de Chine* (rock and small coral heads on sand) NW of *Ilha dos Portugeses*.

### 8. Offshore reefs (about 12 m deep on the shallowest part). *Baixo de Dane* (approx. 25°49'S, 33°E) has still not been investigated because of the distance from Inhaca Island (about one island length north).

## The Bahamas area

Sampling was done with the aid of the submersibles of the Harbor Branch Oceanographic Institution, the Johnson Sea Link I and II operating at 600 m depth in the Bahama Islands. This provides the opportunity of more delicate and precise sampling than the traditionally dredging at large depths without possibilities to control the sampling process. For the locations see Berggren (Thesis-work I, VII)

## RESULTS AND DISCUSSION

### Habitat Selection in Shallow Northern Latitudes (the Swedish West Coast and the Faroe Islands)

The shallow water shrimps which live among algae in northern Europe have a fairly high habitat specificity as is shown in this thesis (Thesis-work XI, X).

The species found amongst algae at the Faroes and in the Gullmar Fjord are listed in relation to their strategy of using the algal zone (Table 1). The species most frequently found in the two different areas, are shown in Figures 4 (Faroe Islands) and 5 (Gullmar Fjord) in percentage with 95% confidence limits (C.I.) for the different habitats.

Table 1. Shrimp species found in connection with algae at the Faroe Islands and in the Gullmar Fjord area. The different species are labelled 1-5, where 5 is the most common and 1 the most rare in the algal zone. The number is followed by an indication of the nature of their stay in the algal zone.

Species	The Faroe Islands	Gullmar Fjord area
<i>Palaemon adspersus</i>		2 - sometimes
<i>Palaemon elegans</i>		2 - sometimes
<i>Athanas nitescens</i>		3 - often
<i>Eualus gaimardii</i>	4 - developmental migration	1 - rare
<i>Eualus occultus</i>		3 - always
<i>Eualus pusiolus</i>	5 - always	
<i>Lebbeus polaris</i>	3 - developmental migration	
<i>Spirontocaris spinus</i>	1 - sometimes	
<i>Hippolyte varians</i>	5 - always	4 - temperature migration
<i>Thoralus cranchii</i>		5 - always
<i>Pandalina brevirostris</i>	2 - sometimes	1 - sometimes
<i>Pandalus montagui</i>	3 - sometimes	1 - sometimes
<i>Crangon crangon</i>		1 - seldom
<i>Sclerocrangon boreas</i>	2 - developmental migration	
<i>Pontophilus bispinosus</i>	2?	

The number of shrimp species in the algal zone is approximately the same at the Faroes as in the Gullmar Fjord but with only one species in common. This species, *Hippolyte varians*, shows in part a difference in coloration between the two areas. In the Gullmar Fjord area a majority of this shrimp lives among brown algae, mostly *Halidrys siliquosa* and *Fucus vesiculosus*, and only a few are found among red algae, as *Delesseria sanguina*, *Phycodrys rubens* and *Polysiphonia* spp.

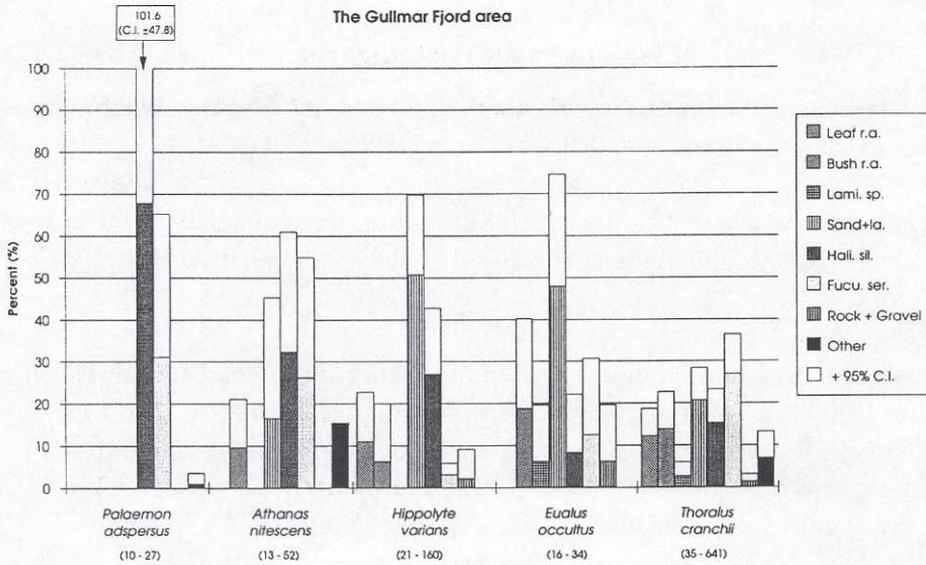


Fig. 3. Barchart of the average percentage with a 95 % C.I. (added on top) of the available habitats used by the shrimps at the Gullmar Fjord area. First number within the brackets under each species name is the number of sampling occasions when the species was collected, number after hyphen is total numbers caught during the whole sampling period.

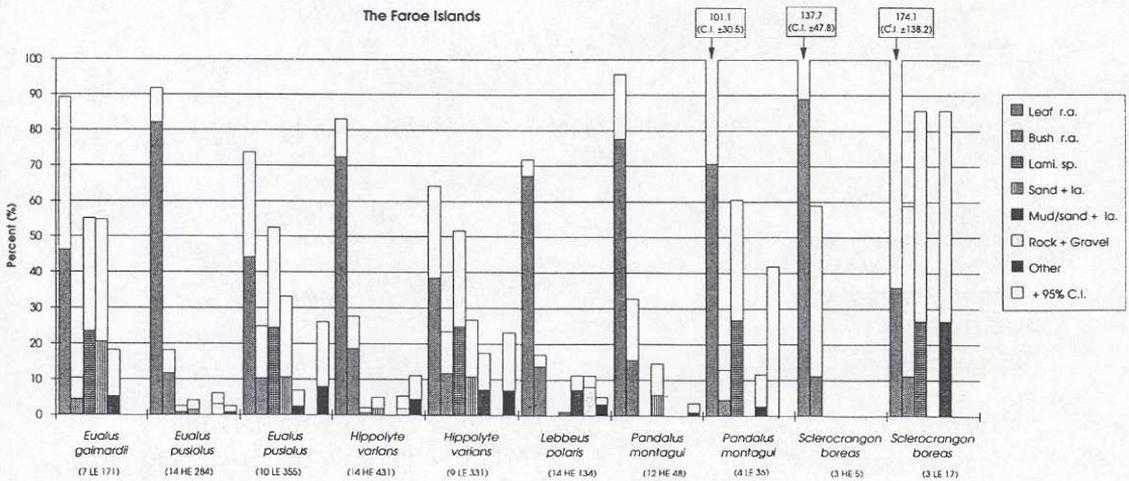


Fig. 4. Barchart of the average percentage with a 95 % C.I. (added on top) of the available habitats used by the shrimps at the Faroe Islands. First number within the brackets under each species name is the number of sampling occasions when the species was collected, HE = high exposure localities, LE = low high exposure localities, last number is the total numbers caught during the whole sampling period.

The coloration of the shrimps from brown algae is evenly yellowish-brown and among red algae unevenly reddish and sometimes with diverse (disruptive) patterns. At the Faroe Islands on the other hand the majority of *H. varians* is found among various species of red algae in highly exposed areas while only few are found among brown algae. In low exposed areas the habitat choice exhibit a similar pattern as the Gullmar Fjord. The colour patterns show the same affinities towards the algal species as in Sweden but the proportions are reverse. Normally the algal shrimps are evenly coloured, blending in with the background algae (Thesis IX). However, those shrimps which are living in 'bush-like' and small 'leaf like' red algae are often showing a disruptive colour pattern (Berggren, unpublished notes). Since an evenly coloured shrimp living among thin algae is more easily found by predators than an irregularly coloured one, selection favours in this respect disruptive coloration.

The habitat choice for most of the species at the Faroes is dominated by a selection of 'leaf formed' red algae. The average percentages of the dominant habitat choices are higher at the Faroes, especially in high exposed localities (HE), and with small 95% C.I. compared to the Gullmar Fjord. A very special type of habitat is the 'loose' algae which are different species of macro algae detached by wave action or other means, drifted down to sheltered areas, in depressions or areas with weak currents on a sand, gravel or mud bottom. In the Gullmar Fjord area the choice of 'loose' algae as one of the dominant habitats takes a high proportion. Use of 'loose' algae must be considered as a very unspecified habitat choice as compared to an algal community, although it is often a complex structure with different algal species involved. The availability on the bottom of this habitat depends on changes in currents and the degradation rate of the algae. This habitat type is frequently found on the bottom in and below the algal zone at the Faroes. However, it was found to have a low priority among the shrimps and this indicates that the selectivity towards a more specialized habitat choice is more pronounced at the Faroes than in the Gullmar Fjord area. (Fig. 4,5 ). This is also indicated by the fact that the similarity levels between the different habitats are higher in the Gullmar Fjord area than at the Faroes. MDS plots of the similarity between the habitats according to sampling for three different species of shrimps (non-juveniles => carapace length > 1.5 mm) in Fig. 6-11. Abbreviations used in the figures as follows: Hs = *Halidrya siliquosa*, Fs = *Fucus serratus*, Lr = 'leaf formed' red algae,

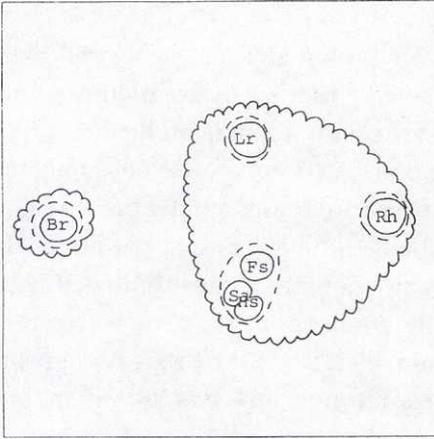


Fig. 6. *Hippolyte varians* - The Gullmar Fjord. Stress: 0.001

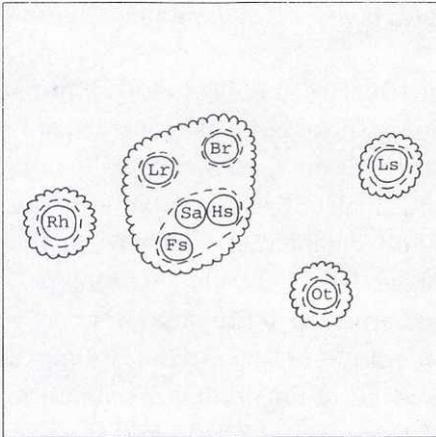


Fig. 7. *Thoralus cranchii* - The Gullmar Fjord. Stress: 0.054

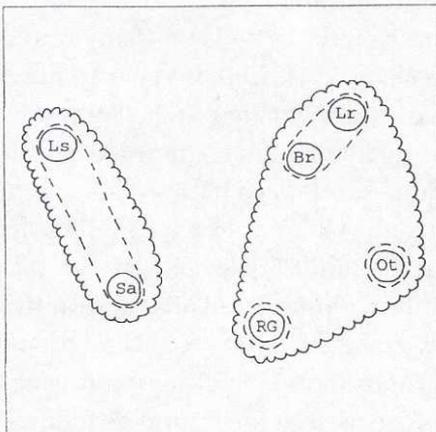


Fig. 8. *Hippolyte varians* - The Faroe Islands (high exposure). Stress: 0.054

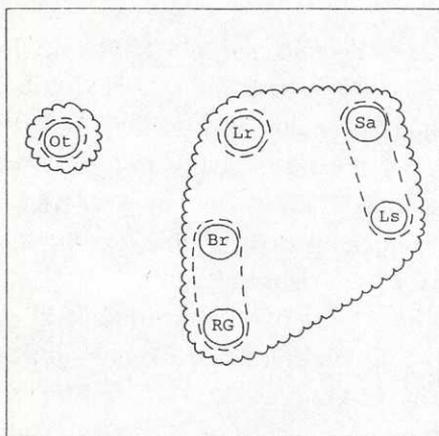


Fig. 9. *Hippolyte varians* - The Faroe Islands (low exposure). Stress: 0.005

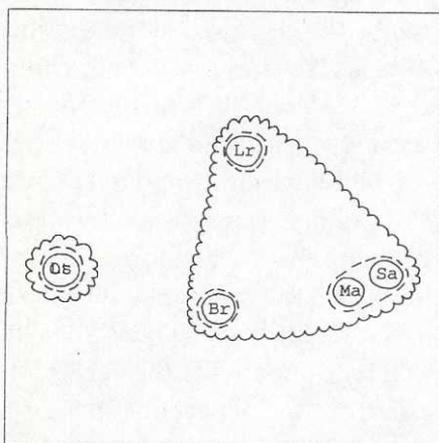


Fig. 10. *Eualus pusiolus* - The Faroe Islands (high exposure). Stress: 0.000

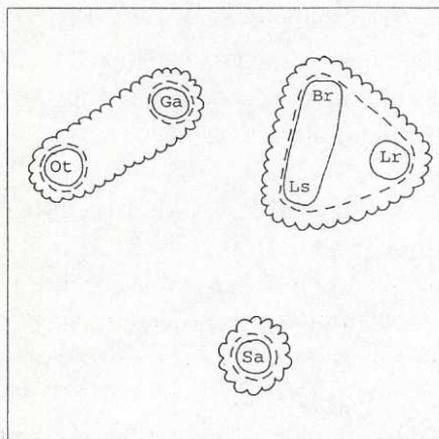


Fig. 11. *Eualus pusiolus* - The Faroe Islands (low exposure). Stress: 0.004

Br = 'bush formed' red algae, Ls = *Laminaria sp.*, Sa = Sand and 'loose' algae, Ma = Mud and 'loose' algae, Rg = Rock and gravel with hydroids and ascideans and Ot = various different habitats used sporadically. Bray-Curtis similarity levels in percent are indicated in figure (wave-formed line = 10 %, dashed line = 30 %, unbroken line = 50 %), the stress level of the graph is indicated in each figure ( $< 0.05 \Rightarrow$  excellent representation of the values,  $< 0.1$  good representation).

This indicates that there is a wider choice of habitats in the Gullmar area, and therefore the shrimps are not as specialized as the ones at the Faroe Islands. The variations in salinity and temperature at 5 to 10 m depth at the Faroes are relatively low (maximum variation: 4 to 12 °C and about 35 ‰ salinity), and very high in the Gullmar Fjord area (maximum variation: -2 to 20 °C and 15 to 35 ‰ salinity). This means that the habitats (macro algae) are affected by the large variations and thereby will not be a stable resource to rely on. The proportion of the different *fascigera* forms (different amount of small seta-tufts on the dorsal side of the carapace and abdominal pleura) in *Hippolyte varians* is suggested to be a function of the degree of variability in salinity and temperature (Thesis-work II). It is shown in the Gullmar Fjord area that *Hippolyte varians* has a much higher proportion of the *fascigera* forms than at the Faroes (Thesis-work X). The Roscoff area in France is an intermediate locality regarding the *fascigera* forms, and it is also intermediate in the variability of temperature and salinity compared to the Faroes and the Gullmar Fjord. The influence of high versus low production (discussed earlier together with environmental stability as factors generating habitat specialists) is maybe of less importance in this case and in waters at these latitudes generally compared to the tropics. From my point of view there is also a problem to separate these factors since low production and low fluctuations are mostly combined in the environment as are high production and fluctuations.

The conclusion is that there seems to be a difference between the Faroe Islands and the Gullmar Fjord area in the habitat selectivity of the shallow water shrimps. This is probably due to a stable conditions with small habitat changes at the Faroe Islands and a much larger environmental variability in the Gullmar Fjord area.

Another indication of the variability in the Gullmar Fjord algal habitats is the obvious seasonal changes in the epiflora of monosiphonal algae on

macroalgae in the upper 6 - 8 m (Thesis-work X). In some years the amount of overgrowth of the macroalgae during the summer, especially in the sheltered areas, cause the algae look like furry tails on the bottom. This overgrowth makes it impossible for the shrimps to remain in that habitat, because they will be tangled in the long fine threads of the epiflora. This coincides with the time of the year when the large and old ones of the population die after their eggs have hatched. The juveniles are still planktonic and the remaining part of the population is spread out deeper down. That makes them hard to find and sample, because they do not perform a habitat shift towards the red algal zone below. The described phenomenon has not been observed at the Faroes by the author.

Crustaceans living in high salinity waters (>30‰) are more tolerant towards low temperatures (Dorgelo 1976). This implies that migrations to deeper areas are normally due to other factors than low temperature. During winter some species of shrimps (primarily *Athanas nitescens*, *Thorulus cranchii* and *Eualus occultus*) remain among the algae in spite of temperatures below zero as shown in Thesis-work X. This indicates that the predator protection of the habitat is a greater advantage than the disadvantage of the loss of motility when remaining at low temperatures. This is in contrast to the shrimps on sand and among *Zostera* (the leaves dies down during winter) which migrate to deeper and warmer water each winter. A few of these shrimps can still be found among algae during winter time, while none is found on unprotected bottom.

During the last glaciation period (more than 16000 years ago) the surface current system in the north Atlantic was different from today. A larval dispersal of the rocky shore fauna from Europe west to Iceland and the Canadian Maritimes was probably promoted during those conditions (Ingolfsson 1992). In addition to the different current patterns in the North-Atlantic during that time, the sea-level was lower than today. One implication of this is that both juveniles and adults must have followed other routes of dispersal than today. The dispersal of shallow water shrimps from the European mainland and the British Isles to the Faroe Islands, is very limited today and thereby the genetic exchange between the populations. Instead the surface currents of the North-East Atlantic promote a larval dispersal from Iceland to the Faroes (Thesis-work IX).

This implies that the shallow water shrimps of the Faroe Islands are relatively old and may form isolated populations in the Atlantic.

#### **Habitat Selection in Shallow Southern Latitudes (Inhaca Island, Moçambique)**

The shrimp fauna of the Western Indian Ocean was earlier assumed to originate from the West Pacific fauna and would therefore be less diverse, but works by Bruce (1974) show that the diversity is greater in the central East African (Kenya and northern Tanzania) region than in the Malaysian-Indonesian region. The high diversity in the Western Indian Ocean may be illustrated by the family *Alpheidae*, which has 142 species in 12 genera in the region (Banner & Banner, 1983) or the subfamily *Pontoniinae* from central East Africa showing 134 species in 35 genera (Bruce, 1974).

Some of the southernmost coral reefs in the world are found in the waters of Inhaca Island, situated at 26°S off the southern coast of Moçambique. The fauna, both on and outside the coral reefs, is very diverse as pointed out in earlier publications (Kalk 1958, MacNae and Kalk 1969) and has attracted scientists in the past to come to this very special locality on the east African coast. Maputo (=Delagoa) Bay, with Inhaca Island as an outer barrier towards the Indian Ocean, is very shallow (average depth 10m) and has a higher temperature than the open sea outside the island. According to the diversity and ecology of the shrimp fauna Maputo Bay is to be interpreted as a tropical enclave in a subtropical/temperate area (Berggren 1993).

Investigations in the Inhaca area have been made by several scientists who have published species lists of various groups of the Crustacea (Barnard 1950, 1955, 1958, 1962, MacNae & Kalk 1958, 1969, Kensley 1981). Most of these works were made from the field station at Inhaca Island (EBM), now administered by the Universidade Eduardo Mondlane (UEM) in Maputo. However, since the late sixties little work on crustaceans and especially shrimps, has been done. All studies on taxonomy and geographical distribution of shrimps in the last 20 years are either done more south (South Africa) or north of the area (Kenya, Madagascar and the islands in the central Western Indian Ocean). The

obvious explanation is the political situation after the liberation of Moçambique and the subsequent war that took place in the country.

This investigation in the shallow waters of Inhaca Island has so far identified 88 species of shrimps in 38 genera. (Table 2).

Table 2. Number of genera and species of Stenopodidean and Caridean shrimps from Inhaca Island and Moçambique compared with Shark Bay, Western Australia.

No	Families / subfamilies	Moçambique				Inhaca Island					Western Australia	
		Total <sup>2</sup>			(Kensley +B&B) <sup>1</sup>	(Berggren) <sup>1</sup>				(M&K) <sup>1</sup>	Shark Bay (Jones) <sup>1</sup>	
		Genus	Species	Assoc. <sup>3</sup>	Species	Genus	Species	New <sup>4</sup>	Missing <sup>5</sup>	Species	Genus	Species
1	Penaeidae	2	7	0	7	2	4	0	3	6	4	15
2	Pasiphaeidae	1	2	0	1	1	1	1	0	0	0	0
3	Bresiliidae	1	1	0	1	0	0	0	0	0	0	0
4	Gnathophyllidae	1	1	0	1	1	1	0	0	1	0	0
5	Hymenoceridae	1	1	1(1)	1	0	0	0	1	1	0	0
6	palaemoninae	2	4	0	2	2	3	1	0	2	1	1
7	pontoniinae	16	44	35(33)	18	15	37	26	3	9	5	5
8	Alpheidae	7	37	18(17)	23	7	29	16	4	13	5	41
9	Hippolytidae	8	11	0	10	5	7	0	1	4	4	4
10	Ogyridae	1	1	0	1	1	1	0	0	1	0	0
11	Processidae	2	5	0	3	2	3	2	2	3	0	0
12	Crangonidae	1	3	0	3	1	1	0	0	1	0	0
13	Stenopodidae	1	1	0	1	1	1	0	0	1	1	1
	SUM:	44	118	54(51)	72	38	88	46	14	42	19	66

- 1) Kensley (1981) and B&B=Banner & Banner (1983), Literature results from the whole Moçambique coast. Berggren, my data of Inhaca shrimps, processed up to now. M&K= MacNae & Kalk (1969), shrimps collected at Inhaca. Jones (1988), Shark Bay data of shrimps.
- 2) List combined of the species from my list together with Banner & Banner (1983), Kensley (1981) and Kalk (1969).
- 3) Associated shrimps on the list, within parenthesis from Inhaca only.
- 4) Species in my list new to Moçambique
- 5) Species missing in my list comparing to MacNae & Kalk (1969)

My list has 28 species in common with the list of 42 species from Inhaca by MacNae & Kalk (1969) and 44 species are shared with the list of 72 species from the whole coast of Moçambique (Banner & Banner 1983,

Kensley 1981). When making a new species list with material from all three lists mentioned, the result will be 118 species in 44 genera. From that list I have so far found 75%, while MacNae & Kalk (1969) only found 36% and the results from Kensley (1981) together with Banner & Banner (1983) sums up 61%. Compared to the literature values for the number of species of littoral shrimps along the whole Moçambiquean coast, my investigation from Inhaca leads to an increase of 39%. It is also conspicuous that 52% of the shrimps in my species list from Inhaca Island have not earlier been reported from Moçambique. These results extend the southern limit considerably for many tropical shrimp species. So far, three new species of caridean shrimps (Berggren, 1991, 1994) and one new mud shrimp (Thalassinidea) has been described (Berggren, 1992).

An interesting feature of shrimps in tropical waters is the high number of species living in association with other animals. Such associations are far more common in tropical (ratio 1:1 or more for associated to non-associated) than non-tropical waters (Bruce 1976a, 1976b). This knowledge can be used for comparisons between areas from different latitudes.

Intimate associations ("commensalism") of Caridean shrimps from Inhaca Island have been found as follows: 51 species associated, 37 species not associated, 14 species unknown if associated. Included in those 14 unknowns are four species of *Alpheus* occurring in partnership with gobiid fishes. It is the fish and not the shrimp that chooses the host and thereby is the associate (Karplus 1981, Karplus *et al.* 1981). This indicates that about 50 % are associated (the 'unknown if associated' is included in the 'not associated'). This is a high percentage that is normally only found in the 'true' tropics, which emphasizes the uniqueness of the area (Thesis-work V). The associated shrimps at Inhaca Island belong mainly to the subfamily Pontoniinae and family Alpheidae.

The definition of the words "commensal" and "commensalism" is given by Gotto (1970): "...organisms which live together, with no harm to either, and which generally share the source of food. ... The advantages are thus one-sided, the commensal being, in effect, a non-paying guest". However, in the work by Duffy (1992) a wider definition is used

denoting that the guest normally benefits from the association while the host is not significantly affected. Patton (1967) describes and discusses various types and degrees of associations (referred as commensalism) in relation to their feeding types. Many of the associated shrimps in the tropics probably feed from the mucus produced by the host and the particles trapped by the mucus. Mucus is not to be considered to be living tissue, but it is produced by the host organism and eating from it means using energy produced by the host. In a strict sense maybe it should be considered as parasitism ("microparasitism"). Gotto (1970) proposes that the pea-crab, *Pinnotheres ostreum*, should be considered to be a parasite rather than a commensal, since it affects the gills of its host, the American oyster (*Crassostrea virginica*). This is true also for the small crab *Pinnaxodes chilensis*, which distorts the test of its sea urchin host, *Strongylocentrotus* sp. (Patton 1967). However, normally nothing is known about the shrimps' way of feeding and living on or in their hosts which makes the labelling of their "life-strategies" very difficult. Since food sharing should be involved in the partnership following Gotto (1970), few cases are as clear as the polychaete worm (*Neris fucata*) living commensally inside the shell of the hermit crab (*Eupagurus bernhardus*). So far the word "associate" with a prefix of the type of host used, has been most adequate when describing these types of partnerships.

The criteria to use when deciding if a shrimp is an associate or not is given by Bruce (1969a): "1. The association with the living host is constant and free-living individuals do not normally occur, 2. All stages of postlarval life are present in or on the host, 3. Adult breeding individuals occur in or on the host, generally in pairs". It could be added to that: I. The association might or might not be beneficial for the host, II. If food is shared, the host must not be affected through starvation (no decrease in growth or reproductive ability), III. If some non-living product from the host (mainly mucus) might be used as a food source it will not have a negative effect on the "host" as pointed out in II. This definition makes it more easy to classify if an animal is associated or not compared to the definition for commensalism. It is normally not advisable to widen or redefine old expression already in use. However, instead of the problematic word commensalism for these types of associations, I propose using the above criteria (1-3 and I - III) and calling it colalism (from the Latin word *cola*: dweller or inhabitant). An associated shrimp would then be called a colal shrimp.

The influences on the hosts from the associated shrimps are normally not very obvious; however, some hosts have a clear benefit from their guests. The movements by the shrimp *Alpheus lottini* Guérin, both when moving around and with the pleopodal beats, will probably cause weak water currents among the branches of its host coral, *Pocillopora* sp. Those water currents can help rinsing away sediments and other particles on the coral. This has often been seen during diving or by observations on shrimps in aquaria at Inhaca by the author. However, sometimes it can be more beneficial than that. In a study by Glynn (1980) *Alpheus lottini* was shown to defend its habitat, the coral *Pocillopora elegans* Dana, against the sea star *Acanthaster planchi* (L.), a corallivore on reef-building corals. *A. lottini* defended its coral host by snapping with the cheliped. The behaviour was elicited both by sight and chemical cues from the predator and was more aggressive in close contact (Glynn 1980). It continued until the sea star retreated. The shrimp can, however, also have a weak negative effect on the growth of the host (coral) in defined areas.

Other coral associates do effect the coral growth, especially those that are found living inside the coral in different ways. An alpheid shrimp, *Alpheus deuteropus* Hilgendorf, is found as cohabiting pairs in fissures of massive coral heads, like *Porites* spp. They hide in exactly fitting *cul-de-sacs* inside the fissures when disturbed. It is not clearly proven if they are excavating the fissure or prohibiting the coral to grow and thereby forming the fissure. The rim of the fissures was found to have a band of hydroids and filamentous red alga. It is speculated that the hydroids might protect the inhabitants, while the algae are used as a standing food crop by the shrimps (Banner & Banner 1982). All fissures in *Porites* that was investigated at Inhaca Island show the above described external characteristics for the fissures. When small samples of coral were brought ashore and cut open along the fissures single individuals or cohabiting pairs of *A. deuteropus* were found, depending on the size of the fissure. The small pontoniid shrimp *Paratypton siebenrocki* Balss (so far not found at Inhaca) is found producing galls in the coral *Acropora* sp. where the pair lives tightly inside the gall with small holes to the outer water, enough for the hatched larvae to escape (Bruce 1969). Their source of food is probably nanno plankton, because, except during the release of the larvae, there is a filtering microalgal mat covering the holes, leaving only minute holes for food items to enter. The few examples

given above show that among these coral associates it is a great difference in the influence on their hosts as well as in the food source. Most coral associated crustaceans are found as male-female pairs (Gotelli and Abele 1983). This is true for most of the associated shrimps in the tropics as well as at Inhaca and especially for those found living inside its host branchial cavity like in molluscs or tunicates. At Inhaca Island outside the Saco area, in one of the tidal banks, the bivalve *Atrina vexillum* is found in dense populations. In random samples taken from that area, the associated shrimps *Anchistus custos* Forskål were found as cohabiting pairs in the branchial cavity of every mussel picked. To detect if there is a pair or only a single individual associated to a host can sometimes be problematic. The shrimp *Dasella herdmaniae* (Lebour) was found in cohabiting pairs as well as single individuals in the branchial cavity of a tunicate at Inhaca Island (Thesis-work II). The single individuals found may be the result of the problem to find both of the individuals inside the dissected tunicate. Another shrimp found as both a pair and a single individual associated to its host is *Athanopsis rubricinctata*, associated to the Echiuroid subfamily Ochetostomatinae (Thesis-work IV). Although, associated shrimps found inside the host or in its burrows might be expected to occur as a cohabiting pair, they are normally locked for life to its host. However, not all associated shrimps are found in cohabiting pairs, for example inside sponges or on alcyonid corals there are lots of shrimps in different sizes and development stages. In my samples from Inhaca these are shrimps of the genus *Periclimenaeus* and *Synalpheus*. According to already referred literature this is also true for other areas of the Indian Ocean. When shrimps do not live in pairs or groups close to the opposite sex, there might be a problem concerning the reproduction. One peculiar case from shallow water (< 3 m) at Inhaca Island is the pontonine shrimp *Periclimenes sonor Nobili*, which is found singly on the sea star *Protocraster lincki* but in small groups of some individuals on the cushion star *Culcita schmideliana*. The very close relative, *Zenopontonia norveca* Kemp is only found singly on *Pentaceraster mammilatus* in deeper waters (12 - 15 m). The sea star hosts of both *Periclimenes sonor* and *Zenopontonia norveca* when found in intermediate depth (5 - 9 m) do not have any associate shrimp. In associations like that it can be problematic for the shrimp to find a partner since they have never been observed outside the host. However, the sea stars are normally found in limited areas where they normally must meet occasionally. An even stranger and more

problematic association is the following an example of. The pontoniinae shrimp *Periclimenes imperator* Bruce 1969, is known to be an obligate associate to the highly motile nudibranch *Hexabranchnus marginatus* Quoy & Gaimard 1832. This shrimp has been reported by MacNae & Kalk from Inhaca Island once, but has not yet been found by me, although the nudibranch has been found occasionally. The shrimp is feeding from material trapped in the mucus of the nudibranch or from the close surroundings it can reach without dismounting. The nudibranch does not respond when the shrimp touched or pinched material from the gill filaments or rhinophores (Shoup 1972). The uniqueness of this species is that they are living individually on the nudibranch and can probably only mate when their host is mating. The nudibranch is not very common and all nudibranchs do not have an associated shrimp. This may explain why the shrimps are so rare. The opposite of single-living can be found for example by the alpheid shrimp *Synalpheus neomeris* De Man. This shrimp has only been found associated to the alcyonarian *Xenia viridis* on the coral reefs of Inhaca Island. *X. viridis* builds small branching colonies about 10-20 cm tall, which are found widely separated on the reef. Normally the shrimps are found in 1 or 2 cohabiting pairs on each coral colony, but sometimes they are found in large numbers and in all sizes on the same host. This community structure is also found from a newly discovered shrimp, associated to a pelagic scyphozoan, *Periclimenes nomadophila* Berggren. They were found in 15 - 30 individuals on the same scyphozoan (Thesis-work VIII). This type of association is unusual since it must involve a very special selection pressure on the shrimp to evolve an association to a pelagic host. The shift from a sessile cnidarian host makes the shrimp rather unique, although its close relatives are associates to corals, sea anemones and to *Cassiopeia* sp., a semi-sessile scyphozoan. To maintain that kind of association implies a very stable and reliable host condition. The current system outside the southern part of east Africa is probably very old and the eddies described in the Thesis-work VIII, maintaining the scyphozoans in the area must then also be old.

The marine area off Inhaca Island seems to be a very complex ecosystem according to its well-developed shrimp fauna. The area is also a receiver of tropical planktonic larvae drifting south in the Moçambique current (Thesis-work V, Walenkamp 1990). From these results it seems that many of the larvae are able to settle and survive in the area. Some has

probably adapted to the new environment and may have formed new species. This means that perhaps some of the new species discovered in the Inhaca area can be endemic to the southern part of Moçambique and will not be found further north or in the south where the environment is less suitable. However, only further investigations can reveal if this is true or not. There is also an interesting comparison to do of the shrimp fauna at Inhaca Island with a locality on the west coast of Australia (Shark Bay) situated at the same latitude (Jones 1988). Shark Bay is a shallow and warm water locality resembling in these aspects of the western beaches of Inhaca Island. Also the majority of the shrimps found are of tropical origin. However, the composition of the shrimp fauna is very different with fewer species totally and the dominating species being digging alpheidids and schooling penaeids. Habitat specialists as the pontoniids are almost entirely missing and the few associated shrimps found (18%) belong mostly to the genus *Synalpheus* and are associated to crinoids and sponges. This implies that the habitats in Shark Bay are less complex compared to Inhaca, with sandy or muddy bottoms and few corals or rocky areas. Even if shrimp larvae of these missing species probably are drifting down from the north, suitable habitats are missing and they can not survive in the area.

#### **Habitat Selection in Deeper Southern Latitudes (Bahama Islands, 600 m)**

Lots of deep sea shrimp species from various expeditions of the past have been described. Unfortunately no or very little information of specific habitats for these shrimps has been revealed (Bruce 1981). I suspect that there are many habitat specialists among the shrimps in deeper waters as well, both on the continental shelves and slopes and on the abyssal plains. I have had the opportunity to examine some deep-sea samples of both host and associated shrimp collected with delicate sampling (the Johnson Sea Link submersibles, Harbor Branch, U.S.A.) which confirms this assumption (Thesis-work I, VII). Bruce (1991) indicates that especially among the pontoniine shrimps, associations to various host species in the deep sea are common. In the deep sea the topography shows micro-variations on the sediment areas that should be remembered when discussing the high diversity on the abyssal plains (Menzies 1965). In all high diversity areas associations can be expected and the deep sea is normally a stable environment and nutrient poor for higher organisms which promote habitat specialists as discussed earlier.

The problem of collecting a reliable sample according to habitat choice or intimate associations starts already below the normal SCUBA depth ( $\approx$  50 m). The use of manned submersibles (operation limits: about 3000 m) nowadays has revealed more associations of shrimps in deeper localities (Bruce 1986 a, b, Thesis-work I, VII).

### Habitat choice and the species concept

Since the habitat choice differs between different shrimp species and is seldom randomly mixed, it must also be important in the speciation process.

According to Gore (1985) some abyssobenthic shrimp species show very small morphological differences while radiating throughout the world oceans. The zoea larvae of these shrimps have been shown to be able to perform vertical migrations of 500 m or more. During these migrations they may be transported by currents longer or shorter distances from the area of hatching. These transportations, continuous or not, allow for a gene flow between widely separated oceanic regions (Gore 1985). In this scenario a slow rate of speciation can be expected with a minor morphological variation between the species. It is also found that some of the decapod crustaceans from the Venezuela Basin show closer morphological resemblance with the species from the Indian or western Pacific Oceans than the eastern Atlantic (Gore 1985).

It is to be expected that species which are geographically isolated from each other but utilizing the same type of habitat will show small morphological changes in the speciation process (Futuyma 1979). This is indicated by a sponge-dwelling shrimp genus, *Spongiocaris* Bruce & Baba, found in 400-600 m depth off South Africa and New Zealand (Bruce & Baba 1973) and at 600 m depth south of the Bahamas (Thesis-work VII), all found as cohabiting pairs in deep-water hexactinellid sponges. These shrimps are utilizing the same type of habitat and maybe also, as shown for the species from Bahamas *S. hexactinellicola*, all have abbreviated larval development. This will make the species (or populations) endemic with close to no possibilities for genetic exchange between different species or populations. This lack of genetic exchange

between the distant populations promote a differentiation into species with small morphological differences. This is shown for the genus *Spongiocaris* in which all three species are very similar morphologically and live associated to the same type of host far away from each other. Being a deep-water genus, *Spongiocaris* might be very old and have given rise to other genera found today. As pointed out both by Bruce & Baba (1973) and Goy (1980), species of *Spongiocaris* seem to be intermediate between *Spongiocola* and *Spongiocoloides*, and all three genera are known to have species living in the internal cavity of hexactinellid sponges. Without more material from different areas on the same depths in-between the finding sites, it is impossible to speculate on the distribution paths. *S. hexactinellicola* shows most resemblance towards the south-African species *S. semiteres*, which have intermediate morphological characters of both the other two species. This may indicate an origin of the genus in the sea south of Africa and a distribution towards the Caribbean area following the shallow mid-Atlantic ridge 50-100 MABP (upper Cretaceous) and a later distribution towards New Zealand.

The ability of shallow-water shrimps to colonize remote areas (islands or distant coastlines) seems to be very efficient judging from the representation of species and genera present. The larvae can show some special adaptations in their ways of dispersal. Some of the tropical littoral caridea have been shown to occur as giant postlarvae in remote areas far from their parent populations. Probably the observed gigantism of larvae, "pelagic bottom forms" (Wilson 1952), is a result of postponed settling while the larvae are transported by the oceanic currents without possibilities to settle. This ability may be an important factor in the colonizations of distant or isolated areas (Bruce 1970). Many of the tropical shrimps show a very high degree of specific associations towards other mostly sessile invertebrates (Bruce 1976), especially in the family Alpheidae and subfamily Pontoniinae. Intimate associations to other organisms may contribute to a higher species richness as shown for example in the genus *Synalpheus* (Duffy 1992). The host specificity for each single species of associated tropical shrimps is normally very high. As an example, in a wide variety of sponges only a few were used by some species of *Synalpheus* in the Caribbean (Duffy 1992).

When dispersing to new areas the associated shrimps can utilize unoccupied niches (hosts). They will thereby establish themselves more safely although with fewer individuals than the free-living ones who encounter more pressure from competition of the well-established species (Patton 1966). These highly specialized shrimp species occur today in most coral reefs in the Indo-West Pacific and some in Hawaii and the Pacific coast of Central America which is probably due to their specialization that enables them to immediately utilize unoccupied niches in their new habitat (Bruce 1978). In other words: in colonizing new areas it is an advantage to be an obligate associate. Associations to a sessile host provide the guest a refuge from predators (Levinton 1982). These close associations, a locked life cycle with its host and pairwise mating on the host only, give a restricted gene flow in the population, thereby limiting the genetic variance of host selection, resulting in that the species chooses the host it is best adapted for. This type of disruptive selection between two or more different host species within a population is likely responsible to enhance a sympatric speciation (Partridge 1978).

The high degree of host specificity is probably one of the major features of evolution of these species (Bruce 1978). When the larvae try to settle not all of them can always find the preferred host species and consequently some must settle on related host species. Most of those constrained associations will probably fail since selection works strongly for the original adaptation. However, since a small genetic plasticity always occurs among sexually reproducing individuals, some might find a related host suitable to live on. If both male and female have succeeded, their offspring will inherit this adaptability towards the new species of host. Most of these will probably be lost back to the original gene pool but some might continue to utilize the new host species. This utilizing of a new host can take two different paths over time: 1 - with a maintained genetic exchange between the old and new population resulting in an increased variety of host species, 2 - no genetic exchange between the populations resulting in an isolated host specialized population. Once the new association is established following case 2 above, the selection will reinforce further speciation. This will probably first be colour pattern and thereafter morphological adaptations towards the new association (Bruce 1978). The colour and pattern differentiation will be a fast change resulting both from a limited genetic variation of the established individuals as from the predator selections. Greater

morphological changes however, with need of a selection pressure to develop, can take a long time. The described speciation process can occur in remote areas from the parent population as discussed earlier. Or the habitat shift can occur in the same distributional area as the parent population. In both cases will the speciation process be fairly fast and short in a geological view. This type of rapid radiation into speciation follows the "punctuated equilibrium" theory, as discussed by Gould and Eldredge (1993).

These strong associations mean that two closely related species apparently may exist sympatrically and yet according to their habitat selection they have an allopatric distribution. As discussed earlier some shrimp species found on related but different host species show only small morphological differences. In some cases the differences can be very minute or not recognized at all and those species will then be classified as sibling species. According to Mayr & Ashlock (1991), sibling species are two species that differ only in minute morphological characters and are probably very old as species. To be able to distinguish between these types of species only very careful observations can detect the small morphological differences that after all normally occur. Today molecular methods provide new tools for studies of sibling species, *e.g.* by using the PCR-(Polymerase Chain Reaction)-method to amplify DNA or RNA from a sample, followed by a gene-sequencing analysis (Machado *et al.* 1993).

The tropical Caridea, and especially the Pontoniinae and Alpheidae show a high number of species which presumably are sibling species or species in the beginning of the speciation process. It is hard to distinguish between such species types without using an interbreeding control. This test should normally give higher breeding success between the intraspecific pairs. This was shown by Knowlton & Mills (1992) with 60% breeding of the intraspecific pairs against 1 % for pairing between the morphs in an experiment on sibling species of the genus *Alpheus* from Panama. The species pairs appear to be found on different hosts and normally with different colour pattern; otherwise they are quite similar. It has also been shown by Knowlton & Mills (1992), in working on some presumably sibling species of *Alpheus* occurring on both coasts of Panama (being separated approx. 3 million years ago by the Panamanian isthmus). Colour patterns seem to be a conservative character within

most shallow-water species of shrimps studied (Bruce 1978). Colour do change according to background and light intensity within certain limits, but the pattern is normally very rigid to changes. What was discussed earlier according to pattern being the first to change in the speciation process is still valid. This because the genetic exchange within a population maintains a dominant pattern and consequently reduces the variability found. However, when a new species has been established the genetic material is more limited and the selection pressure might be somewhat different according to the parent species.

The above shows the importance of careful notes of collected material on both colour pattern and host species, which unfortunately are seldom found in old collected material. Many of the shrimps of unknown associations can be regarded as rare until their hosts are identified and then it might turn out that they are common wherever the host is found.

As a final remark I like to focus on some questions worth while of thinking and discussing upon. These questions are for future works and this thesis can hopefully act as a starter for this. 1) How come that it is the Indo-West Pacific shrimp fauna that is the most species rich? This compared to both the East Pacific and the Atlantic tropical shrimp fauna. In the Indo-West Pacific, the East Pacific and the Atlantic tropical are 93%, 29% and 42% found respectively of the total tropical shallow-water shrimp genera (Bruce 1976). Could one explanation be that the Indo-West Pacific area is the youngest and with the highest number of coral genera (Levinton 1982)? This implies, as discussed earlier, that a very complex habitat can generate more species. 2) Why is there such a difference in the number of associated species between the two subfamilies in the family Palaemonidae? Although the palaemoninae and pontoniinae occur in the same environment, very few of the palaemoninae are found associated while it is the opposite for the pontoniinae. Can it be that the pontoniids have a higher genetic plasticity and thereby being able to radiate to different habitats and consequently forming new species in that process (also applicable for the Alpheidae)? The number of possible sibling species found in the pontoniinae (and Alpheidae) might support that theory.

## CONCLUSIONS

Benthic shrimps in a complex environment show a higher habitat specificity than their counterparts in monotonous or simple environments. Where a complex habitat is found, the numbers of shrimp species in such an area are expected to be much higher than in the surroundings. Within certain limits, low salinity seems to be more limiting in the distribution of shrimps than low temperature. Especially if they have a possibility to live in a suitable habitat.

The shallow-water shrimps in the temperate/subarctic waters are shown to have a specific habitat choice in regarding to the different species of algae found. It is also indicated that they are more habitat specific in a stable (constant) environment comparing to a variable environment (the Faroe Islands vs. the Gullmar Fjord).

The tropical shallow-water shrimps at the east African coast can be found far south in the temperate/subtropical waters (Inhaca Island, Maputo bay) where the habitat show a high complexity.

I believe that with the aid of the submersibles of today, deep-sea samples will reveal many associated species of shrimps from the continental shelves and slopes. Living as an associate on or in another animal will give the shrimp an advantage not only in predatory protection but also in food gathering.

The high number of benthic shrimp species that lives associated in the tropics might be a result of a plasticity in their habitat choice. Thereby will the speciation process occur at a faster rate than compared with the more generalized living shrimps. These shrimps are vulnerable as species since they are dependent of the accessibility of a specified host. However, their plasticity in habitat choice, that might lead to the formation of a new species lowers the competition of the habitats available. To gain the advantage of the associated lifestyle with low predation and a reasonable stable food source, is to try to widen the limited supply of available hosts. The genetic success will therefor be great for those individuals being able to utilize a new host.

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