Symbiotic associations between two anthozoans and crustaceans in the Koster fiord area

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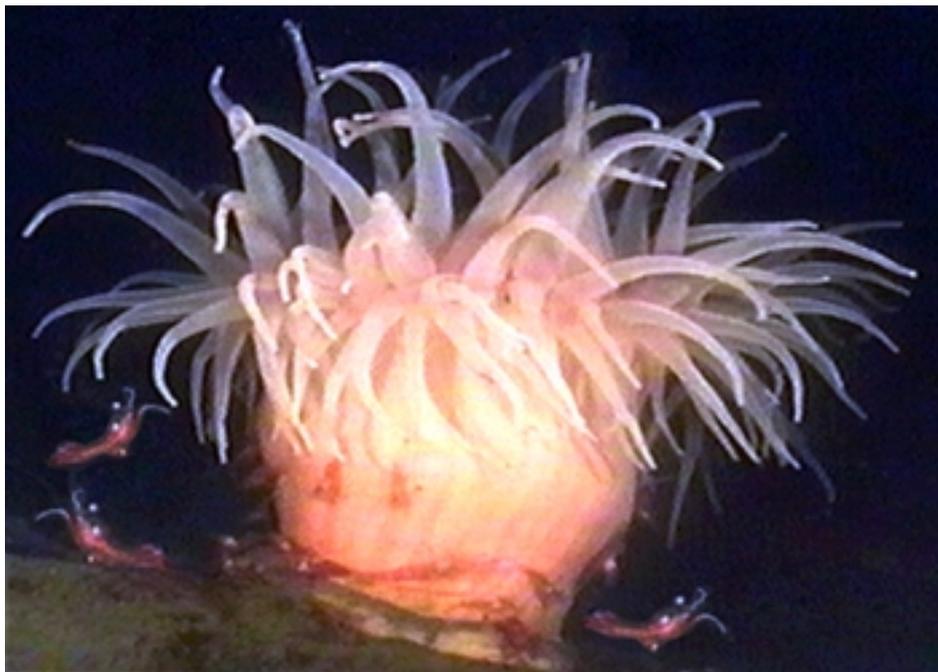
Abstract: While symbiotic associations between sea anemones and crustaceans appear to be common in tropical waters, few such associations are known from temperate waters, except for the symbiosis between hermit crabs and sea anemones. However, for the last two years observations with ROVs (remotely operated vehicles) in the Koster fiord area have suggested that shrimps of certain species (*Spirontocaris liljeborgii, Lebbeus polaris, Pandalus borealis, P. propinquus, P. montagui*) associate with the sea anemone *Bolocera tuediae* and the cerianthid *Pachycerianthus multiplicatus* by aggregating beneath their tentacles. The lithodid crab *Lithodes maja* was also found to associate with *B. tuediae.* In this study, the hypotheses regarding anthozoan-crustacean associations were tested using sequences of video recording by ROVs in situ and laboratory experiments. The results from both the field study and the experiments showed that the crustaceans did have an association with the two anthozoans. The association is presumably a facultative commensalistic association as the crustaceans are all found living as non-symbionts on the sea bottom as well, and the two anthozoans have not to date been perceived as gaining any advantages of the association. *S. liljeborgii* has the closest association with both anthozoans, while *B. tuediae* is the preferred host of all associating species. Reasons for the associations are assumed to be protection from predators, and in the case of the shrimps also an easy access to a food source.

Introduction

In tropical waters symbiotic associations between sea anemones, and fishes and crustaceans are frequent.

In temperate waters in the north-eastern Atlantic and the North Sea the symbiosis between hermit crabs and the sea anemones carried on their shells is well-known, however reports of other associations between sea anemones and crustaceans in these waters have been very few indeed. Vader (1970a) working in Norwegian waters, found amphipods living in the gastrovascular cavity of the sea anemone *Bolocera tuediae*, and copepods associated with the same sea anemone but living as parasites in large, roundish galls, formed from the mesentery walls of the host (Vader 1970b).

The small numbers of associations found between sea anemones and crustaceans in temperate waters might be due to different conditions in these waters which could make symbiosis a less adaptive strategy than in tropical waters. Fautin et al (1995) proposed that the associations between tropical sea anemones and shrimps are a result of adaptations to the particular conditions found in the tropical waters. Another explanation might simply be that observations have been more difficult to make in temperate waters so that, among other things, many symbiotic associations yet have to be discovered.

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Shrimp-actinian symbiosis are usually viewed as commensalistic, the shrimps deriving benefits (food scraps and protection) from their hosts but having no obvious effect on them (Shick 1991).

A few associations have been found to be mutualistic, e.g. in tropical waters between the snapping shrimp *Alpheus armatus* and the sea anemone *Bartholomea annulata*, where the shrimp chases away the polychaete *Harmodice carunculata* which otherwise would predate upon the sea anemone (Smith 1977). The shrimps are typically found near the column of the sea anemone, protected by the tentacles where they are seen feeding on detritus. Both the growth rate and size of the shrimps were found to correlate with the size of the host sea anemone (Knowlton 1979).

Other associations have been found to be parasitic, e.g. between the shrimp *Periclimenes brevicarpalis* and its host sea anemones (at least eight species have been observed as hosts). Both in field and laboratory studies the shrimp has been seen to tear tentacles from its host for food, when deprived of other food sources. In laboratory conditions, the sea anemones would frequently die from this tentacle loss while in the field no "heavy damage" was observed in the host sea anemones. An association that commonly would result in a sea anemone with extremely clipped tentacles, would have to be unstable, so presumably the shrimps "knew" how many tentacles could be tore off before fatally damaging the host sea anemone during normal conditions. The growth, longevity and fecundity of *P. brevicarpalis,* even in the absence of predators, was enhanced by living with its host sea anemone (Fautin et al 1995).

In the tropics most shrimp species associated with sea anemones are found with only some of the species sympatric with them. This implies that shrimps are host species-specific (i.e. able to distinguish between potential hosts and non hosts) (Bruce 1976b in Guo et al 1996).

Guo et al (1996) performed laboratory experiments where shrimps of three species, *Periclimenes ornatus, P. brevicarpalis* and *Thor amboinensis* had to locate their host sea anemone in a Y maze. The result showed that none of the shrimps located a sea anemone by visual cues alone. Instead a significant proportion of the shrimps of all three species were chemically attracted to their host sea anemones, but not to any other species of sea anemones.

Shrimps seem to detect a sea anemone from a distance by diffusing compounds, then switch to cues such as vision, touch, and contact chemosensation (gustation) near the sea anemone.

Many of the tropical symbiotic shrimps and fishes have an obligate association with their sea anemones and are consequently never found without a host (Crawford 1992).

Lysmata grabhami, a shrimp found around Madeira and Canary Islands, has been observed in stable associations with particular sea anemones of the species *Telmatactis cricoides* for up to 13 months. This shrimp species lives in pairs as simultaneous hermaphrodites, a social structure not previously described for any crustacean (Wirtz 1997).

Both mechanical and chemical stimuli are neede to release the nematocysts of a sea anemone. The ability of a compound, from e.g. the exoskeleton of a shrimp, to incite cnidae discharge increases with the amount of mechanical stimulation caused by the shrimp (reviewed by Crawford 1992). Crawford found a slight correlation between time of acclimation to the giant sea anemone *Condylactis gigantea* by the shrimp *Periclemenes anthophilus,* and the length of the shrimps, with shorter shrimps acclimating faster.

O'Connor et al (1977) investigated which species were associated with *P. multiplicatus* in Kilkerrin Bay on the Irish west coast. They found that as many as about 40 animal species associated with the cerianthid. The most conspicious among these were the fan-worm *Myxicola infundibulum,* the bivalvia *Mysella bidentata* and the sipunculid *Golfingia elongata.* The latter association might have been parasitic as nematocysts from the cerianthid were found in the gut of the sipunculid.
They proposed the suitability of the cerianthid tube as a substrate for settlement as the main reason for all these associations, as many of the associating species were not found anywhere else in the research area, except on, or in, the tubes of *P. multiplicatus.* The research area consisted of a soft muddy bottom without any objects to settle on. They defined the associations as commensalistic, as they could not find any advantages for the cerianthid from the associations (O'Connor et al 1977).

In the subtropical parts of the Eastern Atlantic and the Medierranean the spider crab *Inachus phalangium* has a social structure where the females are stationary, associated with the sea anemone *Anemonia sulcata* ,while the males, stationary at day, are travelling around at night visiting the stationary females (Wirtz 1997).
Another variant of associations between sea anemones and crabs was found by Patton (1979). Only the juveniles of the spider crab *Mithrax cinctimanus* associated with sea anemones while the adults were living as non-symbionts. The juveniles were further found to have a rather temporary association with their host sea anemones and often moved on after a single day or a few days.
Even so, during laboratory experiments Patton could observe that *M. cinctimanus* would always move into association with one or another sea anemone rather than hiding under stones or pieces of coral as did non-symbiont species of spider crabs, showing that an association with a sea anemone was strongly preferred. This preference was, however, possibly due to the unnatural conditions in the laboratory, rather than proving a strong association which was not confirmed by the field studies.
The normal position of the spider crab *Stenorhynchus lanceolatus,* associated with the sea anemone *Telmatactis cricoides* at the Canary Islands, was sitting close to the sea anemone, facing outwards, and usually in contact with the sea anemone through placing one or two of the rear legs between the tentacles of the sea anemone (Wirtz 1997).

The deep bottoms (60-250 m) in the Koster fiord area, outside the west coast of Sweden, have been filmed with ROVs (remotely operated vehicles) during a number of occasions over the last two years, and time after time it was observed that shrimps of some specific species *Spirontocaris liljeborgii, Lebbeus polaris, Pandalus borealis, P. propinquus* and *P. montagui*, aggregated beneath *B. tuediae* and *Pachycerianthus multiplicatus* (T. Lundälv pers comm). This suggested that associations similar to the ones between tropical sea anemones and shrimps might exist in temperate waters as well.

However, not only shrimps were seen to associate with *B. tueidae*, but also the lithodid crab *Lithodes maja* was quite often observed sitting beneath the canopy of the tentacles of a *B. tuediae*.

In the present study, a model of a non-random distribution of the shrimp species and the lithodid crab on the sea-bed, is made from the observations in situ with the ROVs. A hypothesis of an symbiotic association is tested, using the *a priori* knowledge from the observations, that shrimps and crabs are aggregating beneath the two anthozoans.

The aim of the study is to investigate some of the more basic questions concerning this newly detected association, such as which species are involved, and to what degree, and what the possible reasons for this symbiosis might be. Further on the associations between sea anemones and crustaceans from temperate waters are compared with similar associations in tropical waters as far as possible.

Materials and methods
Species
The two anthozoans, *B tuediae* and *P. multiplicatus*, are both common in the Koster fiord where depths and bottom substrates are suitable for them. However, *B. tuediae* appears to be the more common species of the two and *P. multiplicatus* was only found in great numbers at certain locations, e.g. south of Yttre Vattenholmen and at Hällsö in the northern part of the fiord.

Type of bottom substrate, but also prevailing bottom currents and the rate of accumulation of sediments seemed to be of great importance to both anthozoans. As a result their distribution was very patchy. At a certain point a dense anthozoan population could be found, and yet only a few hundred meters away only a few individuals would be found.

Only on four occasions were both species found at the same filmed location. The reason for this rare co-occurrence was probably due to the species preferring slightly different habitats.

B. tuediae has numerous large nematocysts on the column, on the tentacles and even on the mesenterial filaments, and is usually described as a voracious predator (Vader 1970a). *P. multiplicatus* has weaker nematocysts and feeds mainly on plankton (pers. observation).

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Five species of shrimps, found associated with the anthozoans, have been identified with certainty, namely *Spirontocaris liljeborgii, Lebbeus polaris, Pandalus borealis, P. propinquus and P. montagui*. Some other species, e.g. *S. spinosus*, may associate with the anthozoans in question, though this species is rarely encountered off the Swedish west coast (Hansson pers comm). If this was the case, those species were not observed or identified during the filmings.

For more information about the species se Appendix A.

Field studies

The field studies were conducted aboard R/V Nereus with two ROVs. The bigger Phantom S4 has a depth range of 300 meters and a cable length of 335 meters. The smaller Phantom XTL has a depth range of 150 meters but a cable length of only 122 meters which restricted its use to a maximum depth of about 100 meters. Each Phantom was equipped with a depth monitor, videocamera, head lights, compass and chronometer and was driven by thrusters at a maximum speed of 2 knots. The Phantom XTL had a Sony EVI-331 colour videocamera and the Phantom S4 had an OSPREY OE1362 colour videocamera.

On R/V Nereus the equipment consisted of a transformer, stabilizing the current from Nereus (and also transforming the 220 V current from R/V Nereus to 110 V for the Phantom XTL). This transformer was connected to the manouvering console from which the ROV was steered and the angles of the camera and the headlights controlled. The video signal from the ROV went to a VCR and was shown on a monitor. The cable connecting the ROV with the manouevering console contained electric wires used to power the camera, the head lights and the engines and sending back signals from the video camera and the instruments.

To ensure that the filmed anthozoans were picked by chance the ROV was steered randomly along the bottom of a chosen site as far as the cable would allow. The area covered in this way was roughly circular. The size of the circle depended on the depth but was usually around 1.800-2.500 square meters.

At each observed *B. tuediae* or *P. multiplicatus* the ROV was stopped and the area immediately around the sea anemone or the cerianthid closely filmed. When the filming was considered adequate to identify all shrimps subjectively judged to be associated with the anthozoan, the ROV was steered to the other side of it via a detour in order to have a complete filming of all shrimps aggregated beneath it.

The control areas, used for comparisons, were chosen randomly from the filming of the sea bed between the anthozoans. This was done by picking an area, shown on the monitor when the tape was arrested after a count of five, after leaving the last anthozoan filmed. This area was subjectively estimated to be of the same size as the areas around the anthozoans.

Most of the filming was done with the Phantom XTL as its camera was of a higher quality and better enabled the identification of the shrimp species.

With the Phantom S4 it was generally only possible to count the number of shrimps beneath the anthozoan but not to identify the shrimps with high enough accuracy. However, some filming was done with the Phantom S4 in order to cover depths greater than 100 m.

Three areas in the Koster fiord were chosen as locations for the filming, one in the south part, including Spiran and Ramskär, one in the middle, including Yttre Vattenholmen, Berggylteskär, Kostergrund and Björns rev (the last one a local non-official name on a deep rock) and one in the north, including Hällsö, Tjurholmen, Kungsviksflaket and Kostersäcken (see Appendix B). Twelve hours of filming were conducted in order to obtain enough material for statistical purposes, though earlier filming and filming for other purposes were used for more general observations of the associations.

Shrimp experiments

In a 54 litre aquarium a transparent dividing glass wall was installed in the middle of the aquarium from one end to a little more than half the length of the aquarium. At the end of this glass wall a second short wall was placed perpendicular to the first, in order to divide the water flow further.

Non-contaminated sea water entered on one side of the glass wall, while on the other side water from an aquarium with either *B. tuediae* or *P. multiplicatus* entered. The water outlet was situated close to the other facing short side of the aquarium to create an even water flow through the aquarium. The water in the aquarium was kept at 8-10 °C. and the room at a constant temperature of 5 °C.

100 *P. borealis* and 12 *S. liljeborgii* were used in the experiments. Ten shrimps were released in the facing short side and allowed to distribute by choice, depending on if they were attracted by the chemical compounds released by the anthozoan or not. By limiting the numbers released at the same time, possible interactions between the shrimps were minimized. Their positions in an area were noted after one hour as they seemed to need this time to choose where to settle down in the aquarium. The areas were defined as: in the release area or in one of the compartments with flows.

In this experiment only chemical compounds from the sea anemone and the cerianthid could be used. Due to difficulties when catching the shrimps, it was not possible to protect them against ultraviolet radiation damaging their eyes. As a result, upon reaching the lab, they were all quite certainly more or less blind. The eyes of deep-living crustaceans show a number of adaptations for vision in low light including the development of a tapetum, superposition optics and large rhabdoms (Land 1981, in Gaten et al 1990). When these crustaceans, which naturally only encounter dim light, are raised to the surface and exposed to sunlight, catastrophic breakdown of the photoreceptors can occur (Nilsson & Lindstrom 1983 in Shelton et al 1985). In the case of

Nephrops norvegicus, exposure to direct sunlight for periods as short as 2 s can damage the eye (Shelton et al 1985).

In a small pilot experiment shrimps were placed in an aquarium with a sea anemone. They approached the sea anemone, presumably attracted by the chemical compounds released by it, but not being able to see the tentacles they bumped into them and violently pulled back, stung by the nematocysts (pers obs). As the shrimps had no perception of the tentacles of the anthozoan, they would not aggregate beneath it, as was observed in the field. Consequently only the possible attraction of the shrimps to the chemical compounds, released by the anthozoans, could be tested for.

Crab experiments

The aim of the experiment was initially to test whether the lithodid crab *L. maja* was interested in finding shelter, and if so to identify the type of shelter they would choose. Would they selectively choose *B. tuediae* as shelter to gain the additional protection from the nematocysts of the sea anemone against predators, or would any kind of shelter do?

An artifical sea anemone was placed in one end and a *B. tuediae* in the other end of a 164 litre aquarium (length 135 cm, width 32 cm).

The artificial sea anemone was used to provide the lithodid crab with a shelter very similar in shape and size to the true sea anemone but without the added protection by the nematocysts of the sea anemone.

The base was made of concrete and buried in the coarse sand covering the bottom of the aquarium. A thick plastic tube served as a column and two different kinds of ropes as tentacles, one that hung down along the column and one that floated above the column in the water. Both ropes were unwound so as to create the impression of a multitude of tentacles.

The water flow entered the aquarium in the middle, close to the bottom and left along the upper edges as the aquarium was allowed to overflow. A dim light was coming from the right. All other possible environmental gradients were considered to be negligible. The water and room temperature were the same as for the shrimp experiments.

One *L. maja* at a time was put down in the middle of the aquarium facing one of the long sides. The area of the aquarium was divided into three sections and it was noted in which section the crab was found at every checking time. The three sections consisted of: 1) immediately around or beneath the fake sea anemone, 2) immediately around or beneath *B. tuediae* or 3) in the middle area of the aquarium not close to any of the shelters. The middle area was of about the same size as the two sheltered areas combined.

The position of each crab was observed after 30 min, one, two, three and twelve hours. In the statistical testing the position after two hours was chosen as the most representative for the purpose of the experiment, i.e. to investigate the need for shelter of the crabs. Two hours seemed to be the time it would take for the crabs to settle down following the initial stress of being

handled and moved to a new habitat, but before they would feel completely at home in the new habitat and thereby loose their presumed need for a shelter. When all the crabs had been tested once the positions of *B. tuediae* and the fake sea anemone were switched around, as it was suspected that the light coming from one side of the aquarium would influence the choices of the crabs.

Only twelve crabs were used altogether as they were difficult to catch, six females and six males. In order to identify the individual crabs they were marked with coloured rubberbands fastened to their rear legs and their weights were noted.

Between the tests, the crabs were kept in a big tank in the same room as the aquarium.

Location and the interaction between location and the choices of the shrimps

Results
Field studies
Video recordings were made at three different locations in the Koster fiord area, namely in the south, middle and north parts of the fiord. A two-way ANOVA in an orthogonal model and with the geographic locations as a random factor and the choices of the shrimps (all species of shrimps pooled together) as a fixed factor, confirmed the generality and similarity of the associations at the three locations (table 1, fig 1). The data showed heterogenous variances according to Cochran's test which, however, disappeared using log-transformation.

Table 1. Two-way orthogonal ANOVA analysing the effect of geographic location (random factor with three levels, north, middle and south part of the Koster fiord), what habitat shrimps of five different species pooled together chose (fixed factor with three levels, *B. tuediae, P. multiplicatus* and control area without any anthozoan. Mean square from the interaction as error term), and finally the interaction of the geographic locations with the choices of the shrimps.

Source	df	Sum of squares	Mean square	F-Value	P-Value	Error term
Location	2	0,580	0,290	1,257	0,3083	Residual
Choices of shrimps	2	12,154	6,077	44,556	0,0018	Loc*choices of..
Location * Choices of shrimps	4	0,546	0,136	0,591	0,6734	Residual
Residual	18	4,153	0,231			
Dependent: log number of shrimps						

showed non significant values (p=0,31 and p=0,67 respectively, n=27). Only the choices of the shrimps was highly significant, p=0,0018.
The post-hoc test (Student-Newman-Keuls) confirmed the significant differences between the choices of the shrimps (table 2).
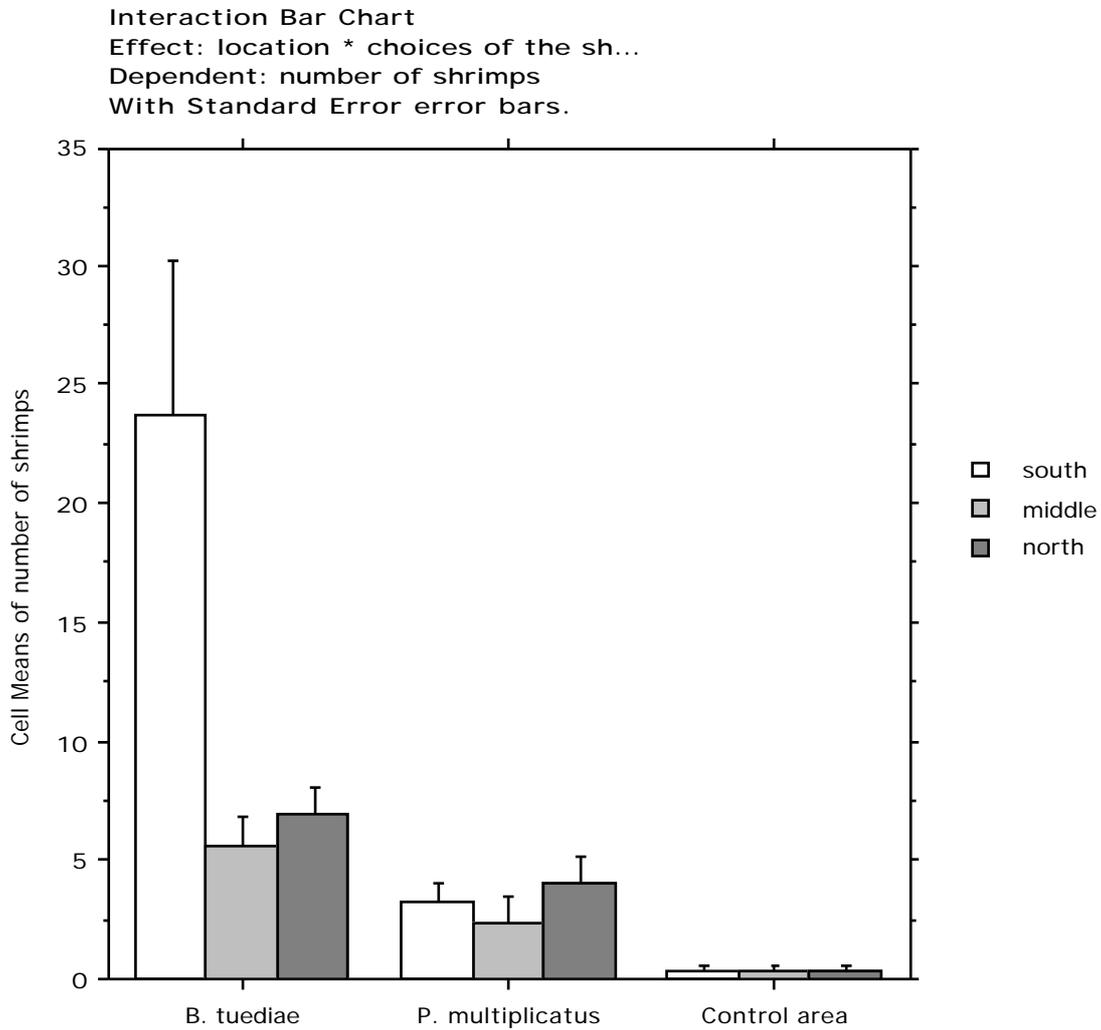
Interaction Bar Chart
Effect: location * choices of the sh...
Dependent: number of shrimps
With Standard Error error bars.

Fig 1. Graph showing how shrimps of five different species pooled together chose between the two anthozoans and the control area at the different geographic locations.

Table 2. Student-Newman-Keuls post-hoc test showing that there was a significant difference of how the shrimps chose between the habitats, *B. tuediae, P. multiplicatus* and control areas.

	Vs.	Difference	Crit. diff.	
Control	P. multiplicatus	1,028	0,484	**S**
Control	B. tuediae	1,625	0,620	**S**
P. multiplicatus	B. tuediae	0,597	0,484	**S**
S=significantly different at this level				

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A total of 96 *B. tuediae* and 36 *P. multiplicatus* were filmed. Of these only seven and six percent respectively were found to be without associating shrimps. Though these percentages might actually be over-estimated as some occasional shrimps around the anthozoans, not filmed from both directions but only passed over with the camera, easily may have been overlooked.

The different species of shrimps were analysed separately to find out which of them that had the closest association with the anthozoans and which of the two anthozoans that was the preferred host. The *Pandalus spp, P. borealis, P, propinquus* and *P. montagui* were pooled together in the statistics, as they could not be separated with certainty on the video tape.

A two-way orthogonal Anova with both host species and shrimp species as fixed factors, showed that there was an interaction between host species and shrimp species, p=0,0042, n=54 (table 3). Thus the significant values for host species and shrimp species were of no interest.

Table 3. Two-way orthogonal ANOVA analysing the effect of host species (fixed factor with two levels, *B. tuediae* and *P. multiplicatus*) and shrimp species (fixed factor with three levels *S. liljeborgii*, *L. polaris* and *Pandalus* spp), and the interaction between host species and shrimp species.

Source	df	Sum of squares	Mean square	F-Value	P-Value
Host species	1	4,807	4,807	12,347	0,0010
Shrimp species	2	58,807	29,403	75,525	0,0001
Host species*Shrimp species	2	4,786	2,393	6,147	0,0042
Residual	48	18,687	0,389		
Dependent: Square number of shrimps					

The significant value for the interaction was probably due to that all shrimp species preferred *B. tuediae* before *P. multiplicatus* but to a different degree, e.g. *S. liljeborgii* associated ca. three times more with *B. tuediae* than with *P. multiplicatus,* while *L. polaris* associated as much as about 50 times more with *B. tuediae* than with the cerianthid (fig 2). The data showed heterogenous variances according to Cochran's test and were thus square-root transformed to make the variance homogenous.

As there was no difference between the geographic locations, they were pooled together, and instead divided into two kinds of habitats, one with a dense population of the anthozoan in question and one with a sparse population of them. An orthogonal two-way ANOVA with both the choices of the shrimps and the kind of habitat as fixed factors, was conducted to see if
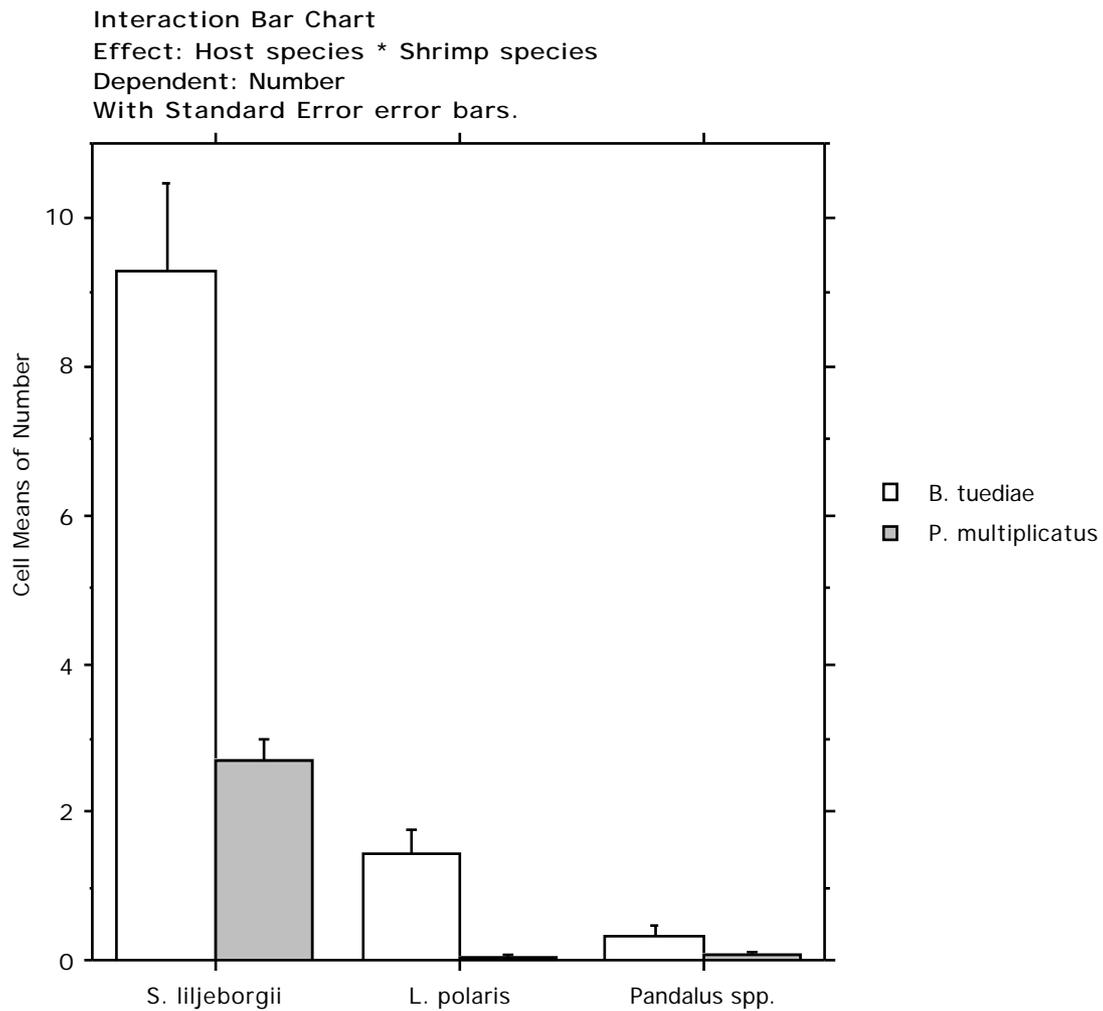
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Interaction Bar Chart
Effect: Host species * Shrimp species
Dependent: Number
With Standard Error error bars.

Fig 2. Graph showing mean number ot the shrimp species, *S. liljeborgii, L. polaris* and *Pandalus spp* observed associating with the two anthozoans, *B. tuediae*, n=52, and *P. multiplicatus,* n=29.

the means of the number of shrimps associating to the anthozoan would differ between these two kinds of habitats. The result gave a non significant result for any difference between them, p=0,89, n=75 (table 4). The data showed heterogenous variances according to Cochran's test and were thus log-transformed.

The lithodid crab *L. maja* was often seen associating with *B. tuediae*. In the video recordings where both species could be observed in the same area 72 percent of the crabs were seen associating to a *B. tuediae* .

Table 4. Two-way orthogonal ANOVA analysing the effect of two kinds of habitats (fixed factor with two levels, sparse or dense populations of anthozoans) and the choices of the shrimps (fixed factor with three levels, *B. tuediae, P. multiplicatus* and control area without any anthozoan) showed a non-significant result, p=0,89, n=75.

Source	df	Sum of squares	Mean square	F-Value	P-Value
Choice of shrimps	2	25,759	12,879	75,044	0,0001
Type of biotope	1	0,003	0,003	0,019	0,8911
Choice of shrimps* type of biotope	2	0,395	0,198	1,152	0,3221
Residual	69	11,842	0,172		
Dependent: log number of shrimps					

Shrimp experiments

The fundamental presumption was that if the shrimps were not attracted to the flows containing chemical compounds from *B. tuediae* or *P. multiplicatus* they were expected to move randomly and distribute evenly among the three compartments of the aquarium made up by the release area and the two flow areas. These three areas were of about equal sizes.

First the shrimps were tested to see if the light coming from one direction affected their choices. A blind test without any anthozoan was conducted. The light was first coming from the same direction as the flows and then from the same direction as the area of release by turning the aquarium 180 degrees. A Fisher exact test gave p=1,00, n=20. Clearly the shrimps were not affected by the light, indeed an expected result as they probably were more or less blind as a consequence of being captured during day-time.

The next experiment tested if blind shrimps were willing to move when attracted by the chemical compounds released by *B. tuediae* or *P. multiplicatus*. A chi-square test gave the result p=0,013, n=92, which indicated that more shrimps stayed in the release area (result 44 of 92, expected 30,7 of 92) than expected by chance alone.

Because of this result the remaining statistical tests only included the shrimps that actually had moved into one of the two compartments with flows, as the shrimps that did remain at the release area were considered less mobile than expected.

The two shrimp species, *P. borealis* and *S. liljeborgii* were tested separately against the two anthozoans to see if these would attract them in a varying degree. The shrimps chose between pure sea water and sea water deriving from the aquarium with either of the anthozoans. *S. liljeborgii* was attracted

by water from *B. tuediae* (p=0,045, chi-square test, n=4) while all the other combinations of shrimp and anthozoan did not deviate significantly from a random choice. However, the significant p-value for the test with *S. liljeborgii* was a bit suspect because of the very small material, though in accordance with the results from the field studies. *P. borealis* tested against both the anthozoans and *S. liljeborgi* tested against *P. multiplicatus* showed non-significant results.

The results from the sea anemone and the cerianthid were then pooled together to see if there was a difference between the two shrimp species in how often they preferred the water flow from any of the anthozoans. (fig 3). *S. liljeborgii* chose the compartments with flows from one of the anthozoans more often than expected (p=0,025, chi-square test, n=5), while this was not the case with *P. borealis*.

The two species of shrimps were then pooled together but with the anthozoans separated to see which anthozoan that was preferred in general by the shrimps. The results though were highly non-significant, p=0,70, n=22, for *B. tuediae* and p=0,40, n=13 for *P. multiplicatus*.
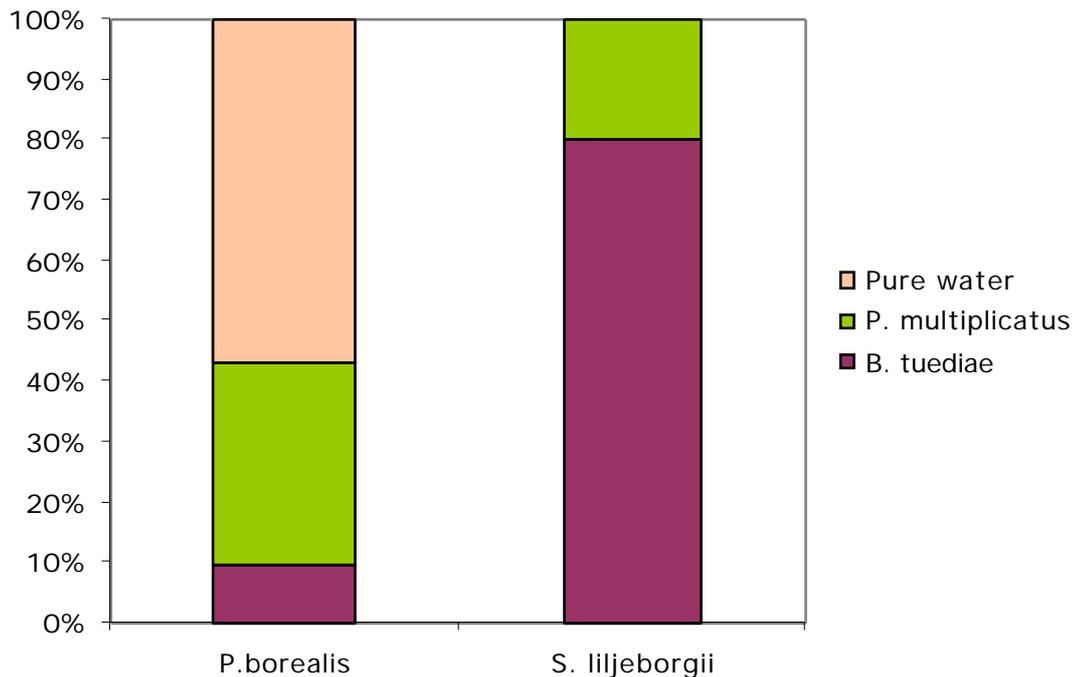

Fig 3. Graph showing how *P. borealis* (n=30) and *S. liljeborgii* (n=5) chose between the flow from one of the anthozoan or pure sea water flow. The graph is in percent as the number of shrimps of the two species were unequal.

The shrimps were also tested so that they could choose directly between the two anthozoans without any possibility to choose pure sea water, but this did not give any significant difference, Fisher exact test p=1,00, n=13.

In another test where the choices of *P. borealis,* n=20, and *S. liljeborgi,* n=7, were directly compared to each other instead of compared to expected choices, Fischer's exact test gave the result p=0,185, i.e. there was no significant difference between the choices of the shrimp species. Even though the result was non significant the graph in fig 4 shows that there might be a weak trend that *P. borealis* more often would chose the flow from *P. multiplicatus,* while *S. liljeborgii* more often would chose the flow from *B. tuediae.* This result disagreed, though, with the results from the field studies, which gave the result that all shrimp species preferred the sea anemone before the cerianthid.
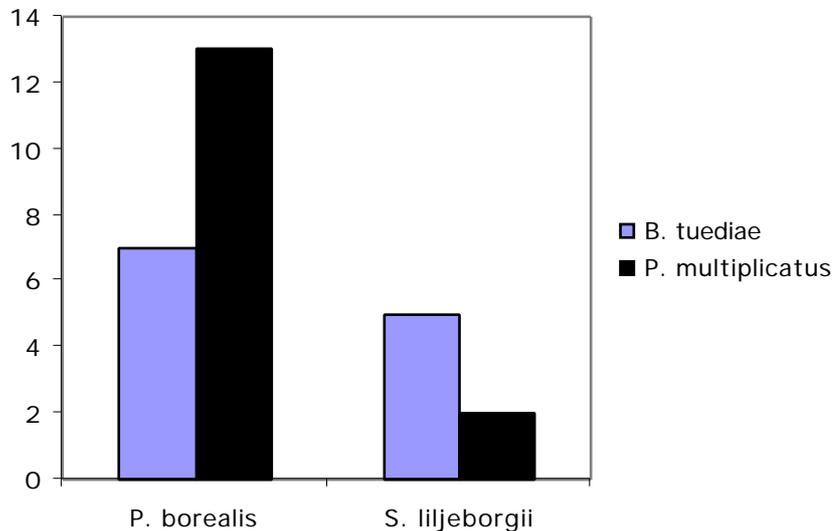

Fig 4. Graph showing the number of the shrimps *P. borealis* (n=20) and *S. liljeborgii* (n=7) choosing the water flows from either *B. tuediae* or *P. multiplicatus.*

Crab experiments

The light was coming from one direction in the laboratory room, which might have influenced the choices of the crabs in the two set-ups of the experiment, one where *B. tuediae* was situated closest to the light source and one where the sea anemone was situated furthest away from it. This was tested for in a likelihood ratio chi-square test, which compared the results directly between the two set-ups. All the time periods, 30 min, one, two, three and twelve hours were compared between the two tests. Only three hours

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gave a significant result p=0,05, while twelve hours showed a trend with p=0,09.

Further on the different time periods were tested directly against each other in a likelihood ratio chi-square test p=0,087, n=12. As there was no significant difference between the the two set-ups in the time-period two hours, neither any significant difference between the time periods, the results of the crabs were hence chosen randomly, six crabs from each of the two set-ups and from the time period two hours, for the remaining statistical tests.Two hours was chosen as the most representative of the choices of the crabs. Before two hours they were perceived as too unsettled in their new environment and after two hours they seemed to feel so secure that they lost their interest for finding a shelter.

If the crabs distributed at random in the aquarium or not was tested for. A non-random distribution would suggest a habitat choice of the crabs. The results from twelve replicate trials showed that the crabs indeed chose to sit close to a shelter, i.e. either a true or a fake sea anemone, p=0,02, n =12.

However, when females and males were tested separately, it became evident that this significance solely was caused by the choices of the females, p=0,01 n=6, compared to the choices of the males p=0,41, n=6 (table 5).

Table 5. Shows how the crabs total, and divided into males and females chose between shelter (either a fake or a true sea anemone) and no shelter, and compared to a random even distribution. Total crabs n=12, males n=6, females n=6. P-values given from chi-square tests.

	Total crabs		Females		Males	
	Observed	Expected	Observed	Expected	Observed	Expected
Shelter	10	6	6	3	4	3
No shelter	2	6	0	3	2	3
P-Value		0,02		0,01		0,41

The last test, was to find out if the crabs actively would choose *B. tuediae* for a shelter, or if any shelter would do. A chi-square test compared how the crabs chose between the *B. tuediae* and the fake sea anemone and compared it to the expected numbers if the crabs had chosen randomly between the two kinds of shelters. For all crabs p=0,003, n=10, for female crabs p=0,004, n=6, and for male crabs p=0,197, n=4. Not surprisingly, considering the earlier result, again the significance for all crabs turned out to be entirely due to the choices of the females (table 6)

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Table 6. Shows how the crabs total, and divided into females and males chose between the true sea anemone and the fake sea anemone, and compared to a random even distribution. Only the crabs that chose shelter, either *B. tuediae* or the fake sea anemone are shown here. Total n=10, females n=6, males n=4. Only six crabs were expected to seek shelter of any type. P-values given from chi-square tests.

	Total crabs		Females		Males	
	Observed	Expected	Observed	Expected	Observed	Expected
B. tuediae	8	3	5	1,5	3	1,5
Fake	2	3	1	1,5	1	1,5
P-Value		0,003		0,004		0,197

Discussion
Field studies

B. tuediae was clearly the most popular host of the two anthozoans for all the observed shrimp species. At the four occasions where both anthozoans were found together at a filmed location, more shrimps were always gathered around *B. tuediae* than around *P. multiplicatus.*

There may be several reasons for this preference; *B. tuediae* was the most common anthozoan of the two, it has the strongest nematocysts and will thus provide a more secure shelter than *P. multiplicatus.* It is also assumed to be extremely long-lived, in accordance with many other actiniarians (Vader 1970a). In New Zealand there is an aquarium record of a small sea anemone more than 300 years old! It is likely that many specimens of the so called "gigantic" tropical sea anemones are at least a century old (Fautin 1992). No information of the longevity of P. multiplicatus was available.

All of the above factors fit very well with the demands Roughgarden (1975) discusses as necessary conditions for a symbiotic association to evolve and for the dependency upon the host by the symbionts. According to him the initial formation of an association occurs when the fitness of a symbiont strategy exceeds that of a free-living or solitary strategy.

For a symbiosis to evolve, three factors must occur:
1. the host should be easy to find
2. the host should survive well with the symbiont
3. the host should provide substantial benefit to the guest.

Furthermore, host dependency increases with the importance and size of the benefits the host provides and the longevity of the host (Roughgarden 1975). The second point in the list above is valid only for mutualism and commensalism, and not parasitism, but probably Roughgarden only included these two forms of symbiosis in his definition.

It would have been interesting to investigate if the shrimp species in this survey would associate with other anthozoans more common than *B. tuediae* and *P. multiplicatus* in other geographical areas. In the deeper parts of the Koster fiord *B. tuediae* and *P. multiplicatus* are the two most common anthozoans. The few sea anemones of other species observed during the filmings were never seen with any shrimps associating to them.

The few *B. tuediae* observed without any shrimps associating to them may have been specimen recently opened up after a period of having had the tentacles withdrawn into the column. Occasionally, individuals of the sea anemone with completely withdrawn tentacles were observed when filming. These withdrawn sea anemones would not provide the shrimps with any significant shelter, and a guess is that the shrimps rather quickly would leave them, trying to find an active sea anemone.

On some occasions, when shrimps were missing underneath the sea anemone, it could simply have been caused by a total absence of any shrimps locally in the area. No information on how long distances the shrimps would travel on the sea bed was available, and so there was no possibility to draw any conclusions of how long a distance they would search for one of the anthozoans in order to find shelter. Or if they would search at all, unless they were able to pick up chemical compounds from another anthozoan.

P. multiplicatus is not able to withdraw its tentacles but instead it withdraws the column into the tube when disturbed so that the tentacles rest directly on the bottom substrate and leave very little space for any shrimps to hide beneath them. In extreme cases the cerianthid is able to withdraw completely down into the sea bed (Lundälv pers. comm.)

Neither *B. tuediae* nor *P. multiplicatus* were perceived to gain any advantages from their associations with the shrimps or crabs during this study, so it is suggested that this association is commensalistic. Whether the shrimps gained any other advantages than protection from predators was not possible to deduce after this short study. Though quite often shrimps could be seen picking in the sediment beneath *B. tuediae* with their pereiopods, presumably finding food particles left from the feeding of the sea anemone or regurgiated by it, thus easy access to food may be another advantage for the shrimps.

Crawford (1992) found that many tropical shrimps have an obligate association with their host sea anemones. This is not true of the shrimp species associating to *B. tuediae* or *P. multiplicatus* in Swedish waters. They are all found living as non-symbionts as well. *Pandalus borealis* and *P. propinquus* are very common on all types of deep bottoms. The other species, *S. liljeborgii* and *L. polaris*, were rarely observed during filming except beneath *B. tuediae* or *P. multiplicatus.* This gave a strong indication of the strength of the association for these species. But as long as even a very few individuals of these species actually were observed in other places than around any of the anthozoans, the association can not be defined as obligate, but facultative. However, it might be speculated that the few specimen of *S. liljeborgii* and *L. polaris* observed not associated with one of the anthozoans, were individuals searching for a new host.

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Most of the shrimp species associating with the anthozoans maintained rather distinct positions in relation to their host. *S. liljeborgii* was observed closest to the column, and in many cases even sitting on the column. In a few cases the shrimps were even filmed sitting among the tentacles. *Pandalus* spp, on the other hand, were typically found sitting in a ring around the sea anemone outside *S. liljeborgii*. Only *L. polaris*, seemed to be flexible in their choice of distance from the column.

Wirtz (1997) investigated for how long individuals of the shrimp *L. grabhami* would stay with their particular host sea anemone. He found that the same individual shrimp could associate with a specific sea anemone for up to 13 months. If the same individual shrimp of the species found in the Koster fiord, would have been found around their specific anthozoan a day later, a week later or a month later from the first video recording, would have been interesting to find out, but for technical reasons this was not feasible.

Though not significant, slightly more shrimps seemed to aggregate around the anthozoans in habitats with sparse populations of these. A rather logical observation, with few anthozoans the shrimps would have to aggregate in larger numbers around the few available to them.

Often when filming a *B. tuediae* there was an abundance of krill, *Meganyctiphanes norvergica,* swimming around the sea anemone, perhaps attracted by the headlight from the ROV. They were probably temporarily blinded by the light and swam straight into the tentacles of the sea anemone, where they immediately were stunned by the nematocysts. The tentacles reacted strongly to the caught krill by quickly curling the tips to ensure the catch.

Sometimes *S. liljeborgii* were observed to become entangled in the tentacles of the sea anemone when they backed away from the ROV or were disturbed by the blinded krill. When, upon contact, the shrimps were stung by the nematocysts of *B. tuediae* they would violently jerk backwards and then directly again assume their normal position, indicating that they were not paralyzed by the discharge of the nematocysts. The sea anemone would typically react to the contact with the shrimp by only a slight contraction of its tentacles, in clear contrast to when the krill were captured by it.

The most important predators on shrimps are the cod (*Gadus morhua*), the haddock (*Melanogrammus aeglifinus)* and the whiting (*Merlangius merlangus*). *P. borealis* is especially predated upon by the hagfish (*Myxine glutinosa)*, while the eel-pout (*Zoarces viviparus)*, guillemots and seals eat *P. montagui* in large numbers in areas where these are found in shallow waters (Smaldon 1979). The populations of cod, haddock and whiting in Swedish waters have decreased because of intensive industrial fishing. This could possibly lead to that the association between anthozoans and shrimps would loose its importance for the shrimps. But smaller fishes like the poor-cod *Trisopterus minutus* and the Norway pout *Boreogadus esmarki* have instead increased in numbers. They are also predators on shrimps, so the need for protection against predators has not diminished for the shrimps, only the species of the predators have changed.

The results from the field studies suggests that both *S. liljeborgii* and the *Pandalus* spp. pick *B. tuediae* as a first hand host, presumably because of their strong nematocysts, though the *Pandalus* spp. keep a somewhat longer distance to the tentacles than *S. liljeborgii.*

L. maja was often found beneath the canopy of the tentacles of a *B. tuediae,* but was never observed beneath a *P. multiplicatus.* If this was because *L. maja* and the cerianthid were allopatric, or if the crab did not approve of *P. multiplicatus* as a shelter could not be concluded, though the latter seems to be more likely. Another possibility might be that *P. multiplicatus* is so sensitive to touch that it immediately contracts into its' tube when *L. maja* try to position itself beneath it.

Predators on *L. maja* may be octopuses which are well-known for their enthusiasm of crustaceans as preys. They are also sensitive to the nematocysts of anthozoans, as shown by the protection hermit crabs are provided by their associations with sea anemones they are carrying on their shells (McClean 1983, Ross 1971). A hypothesis is that the nematocysts *of P. multiplicatus* are too weak to discourage the octopuses, which would then explain why *L. maja* only associates with *B. tuediae* with its stronger nematocysts.

As a rule the crab was always backed up towards the column facing outwards. Their rear end was pressed against the column while their rear legs were circling the column. The same behaviour was shown by the spider crab *S. lanceolatus* (Wirtz 1997). A maximum of three lithodid crabs have been observed sitting around the same sea anemone twice, though a single crab was the most common number.

The lithodid crab *L. maja* did not seem to be percieved as a threat to the shrimps sharing the same sea anemone with them, as they were often seen sitting underneath the crab, on top of the carapax, or walking by very close to the claws of the crab.

While the shrimps were never seen chased away from the sea anemone during a filming sequence, *L. maja* would sometimes, after usually only a short time of filming, leave its typical position at the column of the sea anemone and walk away some distance. If it found the light from the ROV disturbing or if it perceived *B. tuediae* as an ineffective shelter against the ROV was difficult to decide.

Patton (1979) could observe how juveniles of *M. cinctimanus* had rather short-lived associations with their host sea anemones. How long a *L. maja* would stay beneath a particular sea anemone was not possible to find out as the same location was never filmed more than once. Even if it had been possible, the question remains how much the ROV actually disturbed the crabs.

In the field studies, some *L. maja* were seen sitting close to stones, on cliff walls or close to the sponge *Geodia baretti* but only if a *B. tuediae* was not seen nearby. These observations strongly indicate that the lithodid crab indeed preferred *B. tuediae* as a shelter against predators and only would choose stones or sponges as a substitute when no *B. tuediae* was found in the immediate area.

Shrimp experiments

The design of the experiments on shrimp behaviour was essentially the same as that used by Guo et al (1996). A comparison of the results was thus possible. The experiments were conducted with *P. borealis* and *S. liljeborgii* in order to find out if they would locate their host sea anemones in a way similar to the tropical shrimp species, i.e. through detection of the chemical compounds released from the anthozoans.

Unfortunately, as the shrimps were completely blind and very probably not behaving normally, the results from the experiments are a bit dubious. Close to half of the shrimps did not move from the release place at all, significantly more than expected if they had distributed evenly in the aquarium without being attracted to the two anthozoans. It might be argued, that as they were blind, and thus probably unwilling to move at all, the attraction of the chemical compounds from the anthozoans must have been strong indeed to attract even one third of the shrimps.

Crawford (1992) found a certain correlation between the size of the shrimp and the acclimation time to its host sea anemone. This correlation might be one explanation why the smaller and shorter *S. liljeborgii* were found to have a closer association to *B. tuediae*, they simply would not cause such a big discharge of the nematocysts as the *Pandalus* spp. A fact that might have facilitated and strengthened the association into a closer one compared to the association between *B. tuediae* and the *Pandalus* spp.

The results from the aquarium experiments did not show that one anthozoan was favoured before the other as the field studies clearly did, where *B. tuediae* was the preferred host species. The unnatural conditions during the experiments and the low number of shrimps might explain why it was not possible to detect any difference in the experiments.

Crab experiments

Only the juveniles of the spider crabs *Mithrax cinctimanus* and *Hyas araneus* have been found to associate with sea anemones while the adults of these species are non-symbionts (Patton 1979). Unfortunately it was not possible to find any information about at what size *L. maja* starts to reproduce and thereby can be considered as an adult. This made it impossible to test for any differences between juveniles and adults concerning their liability to associate with a *B. tuediae.* During the laboratory experiments the two biggest female crabs carried eggs on two occasions. Both were found beneath the *B. tuediae* when tested, which may indicate that adult *L. maja* in fact associate with *B. tuediae*.

I. phalangium eats food regurgiated by the sea anemone and mucus from the surface of the sea anemone and even crops the tips of the tentacles of the sea anemone (Wirtz & Diesel 1983 in Wirtz 1997). Whether *L. maja* does the same was never observed during the filming or the laboratory experiments.

The females of *I. phalangium* would stay with their particular host sea anemones while the males would be moving around at night searching for the females (Wirtz 1997). If *L. maja* employed the same social structure could not be investigated as all filming was conducted during daytime. Furthermore, it was not possible to identify the gender of the crabs filmed that were found sitting close to *B. tuediae* or moving around on the bottom.

But the crab experiments, though a small material, gave a clear indication that the female crabs were much more inclined to seek protection beneath a shelter, and then especielly beneath a *B. tuediae,* than the males. Possibly, this suggests that *L. maja* may have a similar social structure as *I. phalangium* has.

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Appendix A

Map of the Koster fiord area. Field studies were conducted in three areas.
The north part of the fiord including **Hällsö, Tjurholmen, Kungsviksflaket** and **Kostersäcken.**
The middle part including **Yttre Vattenholmen, Berggylteskär, Kostergrund** and **Björns rev.**
The south part including **Spiran** and **Ramskär.**
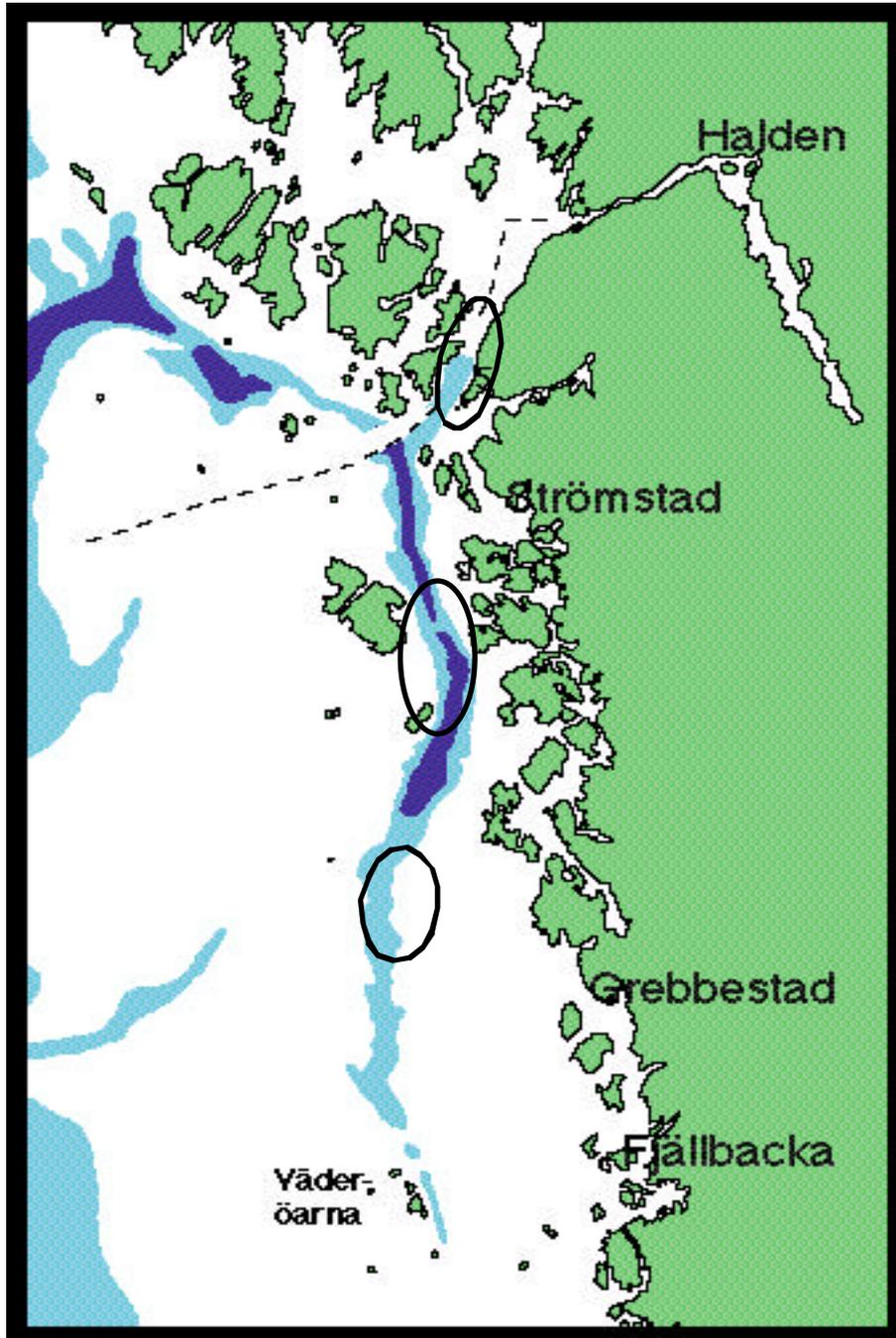
Appendix B
Descriptions of the species in the study

Bolocera tuediae
This sea anemone is found from 20 m down to more than 2000 m and is common on both sides of the northern Atlantic as far north as to the arctic cirle (Manuel 1981).
The colour of the column is usually light red, yellowish orange or sometimes white with the tentacles usually of the same colour as the column but slightly darker and often with faint stripes (Vader 1970). Occasionally specimens with dark purple tentacles were observed during the video recordings. The tentacles are deciduous and are readily shed on occasion, the autotomized tentacles can remain alive for weeks although they are not known to be able to regenerate into new sea anemones (Manuel 1981). The reason for this shedding is unknown but defense against predators have been suggested. The sea anemone has numerous large nematocysts on the column, the tentacles and even on the mesenterial filaments, and it is the only sea anemone in Swedish waters that can be painful to humans (Vader 1970).
The maximum size is about 25 cm. It is probably an extremely long-lived species where the size of mature specimens are dependent mainly on the availability of food (Vader 1970).
The sea anemone is dioecious, the reddish eggs, with a diameter of about 1.1 mm, are among the largest anthozoan eggs known. The pelagic larval develoment takes about one month. In deep water reproduction occurs throughout the year but in more shallow water the reproduction is probably restricted to spring (Vader 1970).
It is usually found on soft sediments mixed with pebbles, shells, stones and cliffs, where it is able to attach itself to the hard substrates, though unattached specimens are observed as well (Vader 1970).
B. tuediae is usually described as a voracious predator and crustaceans like *Pontophilus, Munida, Pandalus, Mysidacea* have been found in the gastrovascular cavities. Once the capture of a small fish, about 10 cm in length, was observed during the video recordings. In the laboratory *B. tuediae* readily accepted fish meat and mussel meat (Vader 1970).

Pachycerianthus multiplicatus
This cerianthid species was not found until 1912 by O. Carlgren in the Trondheim fiord (Dahl 1960).
It is found from 15 m and down to more than 200 m depth at the west coasts of Scandinavia and around Scotland and Ireland (Manuel 1981).
The cerianthid lives on soft muddy sediment bottoms where it is able to dig into the substrate with its tube to anchor itself. The larvae settle after a couple of days from a short pelagic life (Dahl 1960).
The column is often salmon pink and the long whitish tentacles around the edge of the disc are distinctly striped with brown stripes even though completely white specimens have been recorded. The short tentacles around

the mouth are of a single greyish brown colour (Hansson 1998). The maximum size is about 30 cm with the tube an additional 130 cm of which only about ten cm projects above the sediment (O'Connor 1977).

The tube is built by the animal itself. The outer layer (3-7 mm thick) consists of sedimentary debris and is ramified by filamentous algae, the inner layer (2-4 mm thick) is composed of mucous strings and nematocysts derived from the cerianthid itself (O'Connor 1977). The colour of the tube is the same as the sediment, i.e. gray or black.

A very interesting atelia was frequently observed in *P. multiplicatus* when filming them. Very often the cerianthid would slowly turn its tentacle crown towards the direction of the headlights of the ROV, quite similar to a flower turning towards the direction of the sun. Obviously it was able to sense the light. An intriguing fact as the cerianthids usually are found at depths where, at most, only the tiniest amount of sunlight is able to penetrate.

Sea anemones are known to respond to light even though no photoreceptor structures or pigments ever have been identified in them (Shick 1991). Local illumination of the column of *Metridium senile* caused contraction of the parietal muscles in the illuminated (reviewed by Shick 1991). Further research done by North and Pantin (1958 in Shick 1991) and Marks (1976 in Shick 1991) could show that no chemical synaptic transmissions or electrical activity could be recorded during the contractions. Thus it seemed likely that the myoepithelial cells themselves were photosensitive (Shick 1991). As sea anemones and cerianthids are closely related, the same photosensitive system in cerianthids might be assumed.

The question remains, though, for what purpose *P. multiplicatus* uses its light sensitivity! The sea anemone *B. tuediae*, also a deep bottom species like *P. multiplicatus,* has not showed any sign of reaction towards the light when illuminated by the headlights.

Spirontocaris liljeborgii

This shrimp is usually found between 20 and 230 m but has been found as deep as 1200 m. Distribution range is Iceland, Greenland, British Isles, Scandinavia and Massachusetts, North America. Maximum size is 7.4 cm, but it is usually between 4 and 6 cm with the females usually larger than the males. They are found on both hard and soft bottoms. Breeding occurs during winter. The colour is bright red or sometimes dark red. The rostrum has a convex upper margin. This species eats large quantities of foraminiferans (Smaldon 1979).

Pandalus borealis

This is the common commercial shrimp (Nordhavsräkan). It is found between 20 and 900 m depth, frequently between 80 and 500 m. Maximum length is 16 cm, but it is usually about 10 cm. The colour is pale red, and it lives mainly on muddy substrates. *P. borealis* is a protandric hermaphrodite and breeds during winter. Known from the north Atlantic and the Pacific Ocean as far south as 41 degrees North (Smaldon 1979).

Pandalus montagui

This shrimp is also called the Caramel shrimp as it is semi-translucent with red stripes. It is found between 5 and 230 m depth, though seldom deeper than 100 m. The maximum length is 16 cm, but it is usually less than 10 cm. It lives on gravelly, sandy and muddy substrates. It is a protandrous hermaphrodite, males usually developing female characters after 13 to 16 months. They breed during winter. Known from the north Atlantic and north-east Pacific Ocean as far south as 39 degrees North. It feeds largely on the polychaete worm *Sabellaria spinulosa*, but small crustaceans, foraminiferans, hydroids and other polychaetes have been found in the stomach as well (Smaldon 1979).

Pandalus propinquus

It lives from 40 m down to 2000 m depth on hard and soft bottoms. It is red and has a maximum size of 15 cm, though it is usually less than 10 cm. The colour is pale red. This species is dioecious in contrast to the other two *Pandalus* species and it breeds during winter. Its rostrum is strongly curved upwards while the rostrum of *P. borealis* is straight and that of *P. montagui* is slightly curved upwards. Its range is north-east and north-west Atlantic down to 39 degrees North (Smaldon 1979).

Lebbeus polaris

This shrimp is found from 0 m down to 930 m, but usually between 30 and 300 m. The maximum length is 9 cm, though it is usually between 6 and 7 cm. It is transparent with red dots and conspiciously red and white striped legs. Occurs on both hard and muddy substrates. Its range is circumpolar. The breeding season differs in different parts of its geographical range (Smaldon 1979).

Lithodes maja

This crab belongs to the family *Lithodidae* with only this single genus in Swedish waters. DNA-sequencing shows that lithodid crabs are closer related to hermit crabs than to true crabs (pers. comm. H. G. Hansson).
L. maja is found from 10 m. down to 500 m, though usually between 30 and 200 m, on both hard and soft bottoms. Their maximum size is about 15 cm across the carapax. The colour is reddish or reddish brown. Favourite food is brittle stars. The last pair of legs are strongly reduced and difficult to see (Hansson 1998). Carapax and legs are covered with spines, with the juveniles spinier than the adult specimens (Lagerberg 1908). The abdomen is small and slightly asymmetrical, more so in females, reflecting the pagurid ancestry (Hansson 1998). Their distribution range is the north-east Atlantic coast and the coast of east North America.