Algal Preferences in the Masking Behaviour of the Spider Crab, *Notomithrax ursus*

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<u>Acknowledgements:</u>

Abstract

The purpose of this study was to examine the masking preferences of the spider crab, *Notomithrax ursus*. The algal composition of the mask in the natural habitat at Kaikoura was examined to determine the general rules the crab follows when decorating itself. The effects of size and sex on the mask composition were examined, as well as determining how the composition of the mask varies by body part. The preference of the crabs was further examined through the use of choice and background change experiments in the laboratory. It was determined that the preference of certain types of algae for mask material is not entirely dependent on their relative abundance in the environment. Possible explanations for this behaviour are given.

Chapter 1: Introduction

Almost all animals experience predation pressure and have developed many different defense tactics. One important tactic which many different animals rely on for survival is camouflage. Camouflage can consist of "passive traits" like cryptic coloration, or can be caused by behaviors such as mimicry or, the purpose of this study, masking (also called decorating). By using this behaviour, the animal is able to dress up to look like something it is not. In order for camouflage to work as a strategy, there has to be an appropriate match between the animal and its background. The animal can either change itself to match its habitat or move to find a habitat more suitable to its existing appearance. Some animals such as octopuses and some fish can change the color and patterns of their bodies to match their surroundings. Others, especially the crabs of the family Majidae, need to take a more active approach and use materials found in their environment to camouflage themselves (Wicksten, 1993). This behavior is called masking.

Although camouflage background matching is the most obvious benefit of masking, it is not the only one. Masking material can also be used as a food store, chemical or tactile deterrent against predators or even as an escape mechanism (Wicksten, 1993). Masking behavior can also have a cost. Redecoration to match the background can take a relatively long time in some species and represent a period of increased predation risk (Getty and Hazlett, 1978). The benefit of escaping predators has to be weighed against the cost of obtaining decorating materials and sustaining appropriate behavior (Wicksten 1993).

Types of Masking Animals:

Many types of marine invertebrates use masking type behaviors. Species of crab that belong to the Homolidae, Latreilliidae, Dorippidae, Tymolidae and Dromiidae families conceal themselves by covering their carapaces with a sponge, ascidian or anemone held in place by their last pair of modified walking limbs (Wicksten, 1980). This "carrying" behavior is also useful in camouflage against predators (Wicksten, 1986). The crab becomes difficult to see and the covering sponge or ascidians may offer chemical camouflage as well, since these animals are distasteful to many types of fish and other predators (Wicksten, 1986).

Other crustaceans, such as hermit crabs, may conceal themselves through hiding in molluscan shells to which other animals are attached. Larvae of sponges and barnacles settle and then grow to cover the shells. Sea urchins can hold pieces of shell, algae or pebbles over themselves by the use of their spines or tube feet. Insects, such as the assassin bug, can also attach pieces to themselves (Dumont et. al, 2007). As with the Majidae, the value of the "masking" behavior in these species is hypothesized to be protection from predators.

Majidae:

True masking crabs belong to the family Majidae. Spider crabs are a widespread marine family of about 750 species. They can be found world-wide except near Antarctica (Wicksten, 1993). Masking behavior is one of the characteristic behaviors of majid crabs in which crabs attach other sessile organisms, such as anemones, algae,

sponges and hydrozoans, to hooked setae on their carapace after manipulating them with the mouthparts. Hooked setae have only been found in Majidae (Wicksten, 1993) and some Parthenopidae (McLay, personal comment). Decorating is an activity for which the crab is well adapted. The behavior is innate, not learned. Like other crabs, majids release planktonic larval stages into open water (Wicksten, 1993).

Most species of majid crabs eat primarily algae (also the main decorating source), slow-moving or sessile invertebrates and carrion which they pick off the substrate (Wicksten, 1993). They are omnivorous.

Some crabs actively place decorations on themselves, yet many other crabs also tolerate other organisms which passively settle on their carapace (Mastro, 1981). The attachment of decorating material to the exoskeleton is mechanical, not chemical. There is no evidence of an adhesive found after viewing through electron and light microscopes and carrying out chemical tests (Wicksten, 1978).

These crabs can use masking as a defensive tactic because they are slow moving, do not bury, have hooked setae on their carapace and legs, and some species do not shed after the terminal molt at puberty (Sallam et al, 2007).

Most crabs have various cleaning behaviours that involve using their appendages to keep the surface of the animal clean of debris and larval stages of other marine animals. In masking crabs, this behaviour is reversed so that they actively attach pieces of camouflage to their bodies.

Reasons for Masking:

Decorator crabs usually cover their bodies with pieces of algae and other materials. This is especially true of young specimens of the Majidae (Woods & McLay 1994a). Various hypotheses have been presented to account for this behavior but the use of camouflage for protection or food storage has received the most attention (Cruz-Rivera, 2001; Wicksten 1980). The mask can also possibly aid predatory spider crabs in catching prey (Wicksten 1993), increase the crab's apparent size to rivals, and since the pieces of the mask are easily removed, it may aid in the crab's escape from predators. The mask may also contain noxious or unpalatable chemicals to deter predators, or act as a stabilizer in free fall (Sallam et al, 2007).

Wicksten (1980) theorized that decoration behavior may have evolved from setose crabs that fed on detritus they picked off of their exoskeletons. The crabs may then have started attaching uneaten food to their carapace. This behavior may have given them an advantage and may have led to the evolution of true decorating crabs. In addition to the behavior, the pyriform body shape of the masking crabs also had to evolve so that the chelipeds could reach the dorsal surface of the carapace, narrowing at the front and widening at the back.

Generally, smaller crabs decorate more frequently than larger crabs (Bedini, 2002). Small size makes them highly susceptible to predation by fish, so they usually attach pieces of decorating material on an area of the carapace covered with hooked setae (Bedini, 2002). Large spider crabs may reduce amount of covering or may not mask at all. Crabs living in certain depths or on sand have also lost the behavior, possibly

because of the difficulty of finding materials. Juveniles of these species may still mask or at least possess hooked setae (Wicksten, 1993).

Fernandez et al. (1998) examined the variation in the body-covering patterns of the spider crab *Maja squinado* in Northwestern Spain relating to habitat, season, size, terminal molt and migrations. They found that individuals inhabiting shallow zones, which were juveniles, characterized by their small size and frequent molts, had a higher level of decorating behavior and body covering than adults that inhabited deeper areas. In adults (after the terminal molt) they found a decrease in decorating behavior until epibiosis was more common (Fernandez et al., 1998). Epibiosis probably becomes more dominant than self decorating since the absence of molts provided a stable substrate for epibiotic species to develop. However, epibionts can only settle on the crab in the absence of cleaning behaviour.

Similarly the masking crab *Pugettia producta* only exhibits masking behavior as a juvenile. These crabs are active decorators and possess two rows of paired setae on their upper rostrum which serve as attachment sites for decoration materials (Mastro, 1981). As the species grows larger into adulthood, the crab may become less reliant on the protection that camouflage offers and so the ability is lost, or more likely, they come to live in a habitat where there are few masking materials available (Mastro, 1981). Instead, adults fall into a pattern of epibiosis and commonly tolerate organisms that settle on their carapace (Mastro, 1981). The normal cleaning behaviour, which is seen in other kinds of crabs is suppressed (Mastro, 1981).

Stachowicz and Hay (1999) also found that the crab *Libinia dubia* only masks when below a certain size. Adult crabs that have carapace widths that are larger than the

gape size of local predatory fish do not mask at all, in the field or laboratory. They theorize that larger adult crabs may give up the behavior when it is no longer necessary because they are larger than the fish's gape or larger than the fish itself (Stachowicz and Hay, 1999). The behaviour may have been lost in adulthood because no benefit is being conferred. Because this species of crab predominantly uses a rare type of algae, the decorating behaviour may be too costly since the search time to locate the proper materials may be too high (Stachowicz and Hay, 1999).

In addition to crab size, abiotic factors may influence masking behavior, such as geographic variation. A study done on two species of spider crabs (*Micippa platipes* and *Tiarinia cornigera*) along the coast of Japan showed that alga preference and specificity could vary within species at different locations (Hultgren et al., 2006). At the northern location, both species of crab showed little selectivity and used the algae in proportion with their abundance in the habitat. However, at the southern location, *M. platipes* showed a strong preference for the alga *Hypnea pannosa* and both crabs avoided *Corallina pilulifera*. The change in specificity between locations may be due to variation in algal availability (Hultgren et al., 2006).

Thanh et al (2003) showed that the decorating behavior of *T. cornigera* functioned as protection against one of their natural predators; puffer fish. In laboratory experiments, the crabs used more algae for decorating while in the presence of a puffer fish. *Tiarinia* does not eat the algae it decorates with, so it was determined to be a predatory response. Later, Thanh et al (2005) also showed that decorating behavior was increased in the presence of a predator and other conspecifics, suggesting that the presence of a predator may motivate competition for masking materials.

Similarly, Stachowicz and Hay (1999) showed that juveniles of *Libinia dubia* reduce their rate of feeding in the presence of a predator, but not their rate of decorating. This suggests that anti-predator behavior such as decorating takes preference over feeding.

Camouflage:

Using algae for decoration could allow the crabs to blend into their habitat by matching their background or as a way of "looking less like crabs" which would serve as protection against visual predators (Woods and McLay, 1994). With this strategy crabs can gain some protection from visual predators. The camouflage could also enable crabs to ambush unsuspecting prey (Wicksten 1993). Most majid crabs are also nocturnal which also supports the hypothesis that the mask is used mainly for camouflage. During daylight, the only moving parts of resting crabs are the antennae. This motion is concealed by the rostrum, which is usually the most heavily decorated area. At night, the crabs range widely across the seafloor (Wicksten, 1993).

Because the purpose is simply concealment, this behavior is often considered to be non-selective and crabs are assumed to use whatever algae is available. (Cruz-Rivera, 2001). Crabs that use algae primarily to match their background or hide their shape could mask without preference assuming the morphology of the algae available was suitable for use (Cruz-Rivera, 2001).

Camouflage selection could have consequences for the crab. Some primarily herbivorous fish are generalized omnivores that will consume animal matter when available. If the crabs cover themselves with palatable seaweeds, they might be more susceptible to certain predators than crabs that use noxious seaweeds in their mask material (Stachowicz and Hay, 1999).

Thanh et al. (2003) studied the significance of decorating behavior as an antipredator response by using field tethering experiments. The crabs with decoration had significantly higher survival rates than those without decoration after two days in an intertidal rock pool.

Sallam et al. (2007), in studying the masking behavior of the spider crab *Hyastenus hilgendorfi* from the Suez Canal, found that the widespread use of less edible materials (macro-epibionts) for masking purposes suggest that this crab uses its mask primarily for camouflage purposes. The mask seems to make the crab look like its natural habitat, and becomes unrecognizable among the material on the jetties.

Pack (1980) found a significant difference in the number of decorated versus undecorated *Notomithrax ursus* that were attacked and killed by octopus, suggesting that decorating does help in avoiding predation.

Rodolfo (1987) found that the substrate selection and decorating behavior in *Acanthoonyx petiveri* related to exoskeleton color. The crabs slowly gained pigment in their exoskeletons after molting to match the color of their habitat. However, since this could take a few molts, they also used decorating behavior for a quicker way of camouflaging.

Food storage:

An alternative theory of masking behavior is that crabs can attach algae to their bodies as a means of storing food for later consumption and therefore would benefit from masking with the types of algae that they prefer to eat (Cruz-Rivera, 2001). Interactions between feeding and decorating behavior can be doubly advantageous to the fitness of the crab. Since the mask material continues to grow (Woods and McLay, 1994), the mask may serve as a renewable food resource which would allow the crab to decrease energy expenditure and risk of predation by having to locate its own food supply (Kilar and Lou, 1986).

The food storage theory is unlike the camouflage theory in that it requires crabs to exhibit some selectivity about their mask material, since storing unpalatable (to itself) materials would give them little benefit (Cruz-Rivera, 2001).

Crabs that are only using the mask as a food store will most likely hide during the day when visual predators are active, or will place algae in a way that doesn't provide concealment to the crab (Mastro, 1981) which would reduce the potential of the algae for protective cover (Cruz-Rivera, 2001). Cruz-Rivera (2001) found that in three species of crab found along the Mediterranean coast of Spain, the preferences for decorating material did not match the preference algae as a food source.

Kilar and Lou (1986) carried out an experiment on the dietary and camouflage preferences of the decorator crab *Microphrys bicornutus* on a Caribbean fringing reef. Their experiments showed that this crab prefers to not eat its camouflage when other foods are available, but when food is scarce, it will readily consume its mask. The carapace flora serves as an alternative food reserve in this species.

Mastro (1981) showed that the majid crab *Pugettia producta* used its mask for food. The crab eats the algae off of its own rostrum when it is isolated from food. Also, the algae is only located on the rostrum and may successfully conceal the rostrum, but rarely breaks up the outline of the rest of the body and could not be providing sufficient camouflage. Therefore, the decorating behavior must have a relationship only to feeding.

Food and masking preference were also investigated in the majid crab *Inachus phalangium*. It was discovered that although decoration was used as a short-term food store, the crab exploited the algal nutritional and chemical properties differently. Food preferences and mask preferences were decoupled. The crab preferred to eat red and green algae, while preferring to dress up in brown algae (Rorandelli et al 2007). This crab also closely associates with anemones, from which it gets protection.

Chemical Defense:

Selectivity may be important for crabs that live in areas where omnivorous fishes are the main algal grazers and predators. The crabs may gain protection from choosing mask materials that are of low preference or noxious to the predatory fishes (Cruz-Rivera, 2001). By behaviorally sequestering these defenses from chemically noxious species, small crabs may reduce their susceptibility to predation (Stachowicz and Hay, 1999). Camouflage behavior mediated by noxious plant metabolites might be more effective than visual camouflage because the crab would appear to be an item that is unpalatable and avoided. If discovered and taken into a predator's mouth, the chemicals might cause the predator to reject the algae and therefore the crab (Stachowicz and Hay, 1999).

Other Defense Mechanisms:

The mask may have other defense mechanisms besides as a food storage, camouflage or chemical deterrent. The pieces of the mask are easily detached and so might aid in the escape from a predator, who finds it has only a piece of seaweed in its mouth instead of a crab. Also, the mask may serve as free-fall stabilizer underwater (Wicksten, 1980). It has also been suggested that the mask may serve a purpose in intraspecific encounters such as mating behavior and rivalries, although this is pure speculation with no evidence to support it. The mask may also make predators consider the crab an unworthy food source because they will taste and feel like algae and this might cause the predator to spit them out (Wicksten, 1993).

Notomithrax ursus

Notomithrax ursus is a masking crab that is distributed around Southeast Australia and New Zealand. It has a bathymetric range extending from the intertidal down to about 75m (McLay, 1988). *Notomithrax ursus* is commonly found under rocks in the intertidal zone, usually thickly covered in red and brown algae. Crabs collected from deeper water are not usually masked (Woods and McLay, 1994a). *N. ursus* is nocturnal, remains hidden and relatively motionless until night time when it comes out from hiding to feed and move around. Being nocturnal may enable it to avoid most visually hunting predators. The carapace of *N. ursus,* even with a sparse covering of algae, appears to be well camouflaged because of its dense covering of long setae, epibionts and silt that collects among the setae.

Description of masking behavior**:**

Notomithrax ursus' masking behavior starts when the crab finds a clump of algae. The crab selects a single piece of the algae and using its chela, "measures" a piece to the required size. The crab then snips off the piece of algae and transfers it to its mouthparts where the cut end is trimmed of any projections. One cheliped is then used to transfer the piece to a part of the body. The crab attaches the seaweed by rubbing it against the hooked setae so that the cut end becomes entrapped by the hooked setae. In this case, the setae function much like "Velcro" attachments. Branched algae are inserted between and held by the hooked setae. Thallose algae, such as *Ulva* sp. may be inserted between the setae or impaled on them. (Woods and McLay, 1994a). The pieces are always applied in the same sequence, starting with the rostrum and proceeding backwards down the carapace and then backwards on the legs (Woods and McLay 1994a).

The distribution pattern of masking and the number of pieces used does not change with crab size. The average length of each piece applied increases as the crabs get bigger. *N. ursus* prefers to mask with branched algae, rather than thallose algae. The mask of *N. ursus* serves to make it look like a clump of seaweed (Woods and McLay, 1994a). Woods and McLay (1994b) found that *N. ursus* commonly uses the algal mask as a source of food. There is a dual role between camouflage and food storage. However, camouflage is probably most important since food consumption only makes up a minor part of the mask turnover (Woods and McLay, 1994a).

In this thesis, I will examine more closely the algal preferences of the spider crab *Notomithrax ursus* for masking behavior. The masking behavior in the field and in the laboratory was examined to gain some insight into what preferences the crab has for

decorating algae depending on the type available, if the preference changes with sex or size and if there is a particular pattern of distribution of the algae on the crab's body.

Chapter 2: Natural Cover

Introduction:

The purpose of this study was to do a survey of the mask composition of *Notomithrax ursus* in its natural environment. These data was then analyzed to determine the types of material used in the mask and the relative frequencies of each material. The mask composition data were also compared by size and sex of the crabs to determine the effects these traits might have on the masking behaviour. The composition of the mask on each body part of the crab was also examined to see how the algal properties change depending on their placement on the body.

Methods:

To examine the natural mask composition of *Notomithrax ursus*, crabs were collected from intertidal areas at Kaikoura, New Zealand. For each crab, the sex and carapace width (C.W.) were recorded. The sample includes 33 females and 35 males and sizes ranging from 12 mm and 42 mm C.W. Crabs missing limbs were not included. For each crab separately, each piece of algae in the mask was removed with forceps and the species was determined, the length was measured and the body part to which it was attached was recorded. The mask data were collected within a day of removing the crabs from their natural habitat to ensure minimal mask loss or turnover. All crabs were returned to the collection site after the mask data were obtained.

Results:

Mask Composition

A total of 21 species of algae and hydroids were identified in the mask composition of *Notomithrax ursus* in the wild. Of these species, eleven were rare occurrences – only found on one of the 68 crabs surveyed. Seven others were found on multiple (but still less than 50%) of the crabs, but usually only 1 or 2 pieces in the entire mask. Three species of algae, identified as *Euptilota formosissima*, *Plocamium microcladioides* and *Halopteris virgata*, by far made up the majority of the mask on all crabs (Table 2.1). were found on the vast majority of crabs (Figure 2.2). These three species also were found on the vast majority of crabs (Figure 2.2). *Euptilota formosissima* and *Plocamium microcladioides* are red algae, *Halopteris virgata* is a brown alga.

Effects of Crab Size

The number of pieces in the mask was found to not change significantly with crab size (Figure 2.3, $r^2 = 0.05$) for either males or females. However, the length of each piece in the mask did increase significantly as crab size increased (Figure 2.4, $r^2 = 0.74$).

The number of pieces of *Euptilota* and *Plocamium* did not vary with crab size ($r^2 = 0.03$ and $r^2 = 0.06$ respectively; Figure 2.5). However, the number of pieces of *Halopteris* did decrease significantly as crab size increased ($r^2 = 0.19$, Figure 2.5). The

length per piece of each algae species all increased as crab size increased (Figure 2.6). The length of each *Euptilota* and *Plocamium* piece was significantly larger than the average length of each *Halopteris* piece (Two- way ANOVA, p < 0.001).

Effect of Sex

There was no significant difference in the number of pieces used between males and females (t-test, t = 1.91, p = 0.056; Figure 2.3). There was also no significant difference in the length per piece of algae used in the mask between males and females (t-test, t = 1.935, p = 0.053; Figure 2.4).

There were some differences in the mask composition between the sexes. There was no significant difference in the amount of *Halopteris* used in the mask by each sex (t-test, t = 1.04, p = 0.30). There was also no significant difference in the amount of *Euptilota* used in the mask by each sex (t-test, t = 0.829, p = 0.407). Also, the sexes did not differ significantly in the amount of other species present in the mask (t-test, t = 1.539, p = 0.12). However, males used significantly more *Plocamium* than females (t-test, t = 2.819, p = 0.005).

Distribution of Algae on the Body

Table 2.2 shows the average combined lengths of all the algae on each body part of the crab. The crabs had four times as much mask material on the carapace as on the

front legs. The amount of algae on the legs was highest on the front legs, and decreased posteriorly.

Table 2.3 shows the average number of pieces of algae on each body part of the crab. The carapace contained the most pieces (16.40). Similar to the lengths of algae, the number of pieces on the legs decreased from the front to back of the crab.

The species composition varied on different body parts of the crab as well. The mask on the carapace and front legs of the crab was predominantly made up of the red algae, *Plocamium* and *Euptilota*. However, towards the back of the crab, the percentage mask composition of *Halopteris* increased until that was the predominant species on the fourth legs (Figure 2.7, Table 2.4). Although the percentage of *Halopteris* in the mask increased towards the back of the crab, the total length did not. Figure 2.8 shows that the total length of *Halopteris* on each body part remains relatively constant. It is the amount of *Euptilota* and *Plocamium* that decrease toward the back of the crab, rather than *Halopteris* increasing.

Similarly, the number of pieces of *Halopteris* also remains nearly constant across the body of the crab. The only significant difference is between R1-L4 (Two-way ANOVA, f = 7.11, p = 0.005, Figure 2.10). However, because the number of pieces of *Euptilota* and *Plocamium* decrease significantly (p <0.0001), the percentage of *Halopteris* pieces towards the back of the crab increases (Figure 2.9, Table 2.5).

Discussion

Mask Composition:

The mask of *Notomithrax ursus* was predominantly composed of only three species of algae, two species of red algae, *Euptilota formosissima*, *Plocamium microcladioides* and one species of brown algae *Halopteris virgata*. Various other species of algae were also found in the mask, although not in very large numbers.

Interestingly, of the three most commonly used species, only *Halopteris* is actually found growing attached in the habitat in which the crabs live. *Euptilota* and *Plocamium* species grow in deeper water, not in the intertidal zone where the crabs were collected. One of the most abundant types of algae growing at the collection site was *Ulva*, a green, thallose algae. Despite being a very common species, this alga was found in the mask of only about 12% of the crabs collected. A closely related and co-occurring species of spider crab, *Notomithrax peronii*, is seen to commonly use *Ulva* in its masking material (personal observation).

These three species of algae may not be the most abundant growing naturally in the crab's environment. However, since *Euptilota* and *Plocamium* are present in the habitat only when washed up from deeper water, they may be more often present lodged under the rocks where the crabs hide, and are thus more easily accessible than algae that

is actually growing on top of the rocks. The general absence of *Ulva* in the mask cannot be explained by this, since it is also often washed up under rocks.

Notomithrax ursus may be preferentially choosing algae based on ease of use. Certainly in the environment where the crabs were collected, *Halopteris*, *Plocamium* and *Euptilota* were by far the most abundant species of algae delicate and soft enough for the crabs use, although not most abundant overall. Many of the other types of algae present, such as the kelp, are far too large and tough for the crabs to manipulate with their chelipeds or mouthparts.   This may also explain the lack of *Ulva* in the mask. The crabs are able to cut and manipulate *Ulva*, but it may be not be as efficient as the other types of algae. *Ulva*, being a thallose type of algae, has a greater width that needs to be cut than the filamentous types. The attachment sites on the crab's body may also not be ideal for this type of algae. *Notomithrax peronii*, which does use *Ulva* in its mask, differs in the way it attaches each piece of algae, which may explain the discrepancy in preference. Even though *N. peronii* has hooked setae like *N. ursus*, they tend to impale each piece of algae instead of hooking it between the setae. Also, *N. ursus* generally attaches the cut end of the algae to the setae, whereas *N. peronii* is less discriminate and will attach at either end or even in the middle of the piece.

The preference may also be explained by seasonal variation. There is less seasonal variation in the amount of *Halopteris*, *Plocamium* and *Euptilota* washed up on the shore than *Ulva* which tends to vary greatly in abundance (personal observation). It may not be advantageous to dress up in a species that is not always present in the environment. This, however, does not explain why *N. peronii* still continue to use it. It is possible but not known if there is seasonal variation in the use of *Ulva* by *N. peronii*.

Effects of Crab Size

The crabs were shown to compensate for an increase in size by increasing the average length of each piece of algae used. There was no correlation between the number of pieces of algae used in the mask and carapace width. This suggests that the number of attachment sites for decoration is limited, so the crabs must increase the length of each piece to provide their larger bodies with adequate cover.

The fact that the natural mask composition changes with size may be also due to the ease of use of certain types of algae. The percentage of *Halopteris* in the mask was shown to decrease with carapace width. Because of its structure, it may be harder for the crab to cut suitably large stable pieces than the more "solid" algae like *Euptilota* and *Plocamium*. Since *Halopteris* is composed of fibers attached to a central stalk, it has a greater tendency to crumble as the pieces get too large. *Euptilota* and *Plocamium* may also simply grow to a larger size than *Halopteris*.

The cover necessary for a larger crab may also be more easily obtained by using *Euptilota* or *Plocamium*. Because of their "fanning" structure, a longer piece also generally provides a greater width of cover. *Halopteris*, on the other hand, branches infrequently, so typically the piece remains the same thickness across the entire length.

Effect of Sex

There was no correlation between sex and the amount or size of algae used. There was, however, a significant difference in the mask composition in one type of algae. Male crabs used significantly more *Plocamium* than did female crabs. The remaining species were used in similar amounts. This effect cannot be explained by the larger size of male crabs, since the amount of *Plocamium* in the mask was shown not to vary with size.

Distribution of Mask Materials on the Body

The amount of algae used in the mask on each body part did vary significantly depending on the location. On average, the crab uses four times as much length of algae on the carapace as on each first leg. The amount of algae used per leg decreases as you go towards the back of the crab. The fourth leg contains only half as much algae by length as the first leg.

The number of pieces used in the mask also depends on the body part on which it is located, with the largest number being located on the carapace, probably because the carapace has the greatest area, then the first legs and so on. The average size per piece also differs, but only on the carapace. The pieces on the carapace had an average length of 24.44 mm, and each of the legs had an average length per piece of ~13 mm. The average size of each piece on the legs was similar to each other – but the number of pieces used increased. The fact that the crabs seem to compensate for the varying size of

their appendages by using more pieces instead of larger pieces, is contradictory to the pattern they have as a whole – that when carapace width increases, the average overall length per piece increases instead of the number. This may imply that the number of attachment sites on the legs varies with the size of the leg, with the front legs having a greater number of attachment sites than the back.
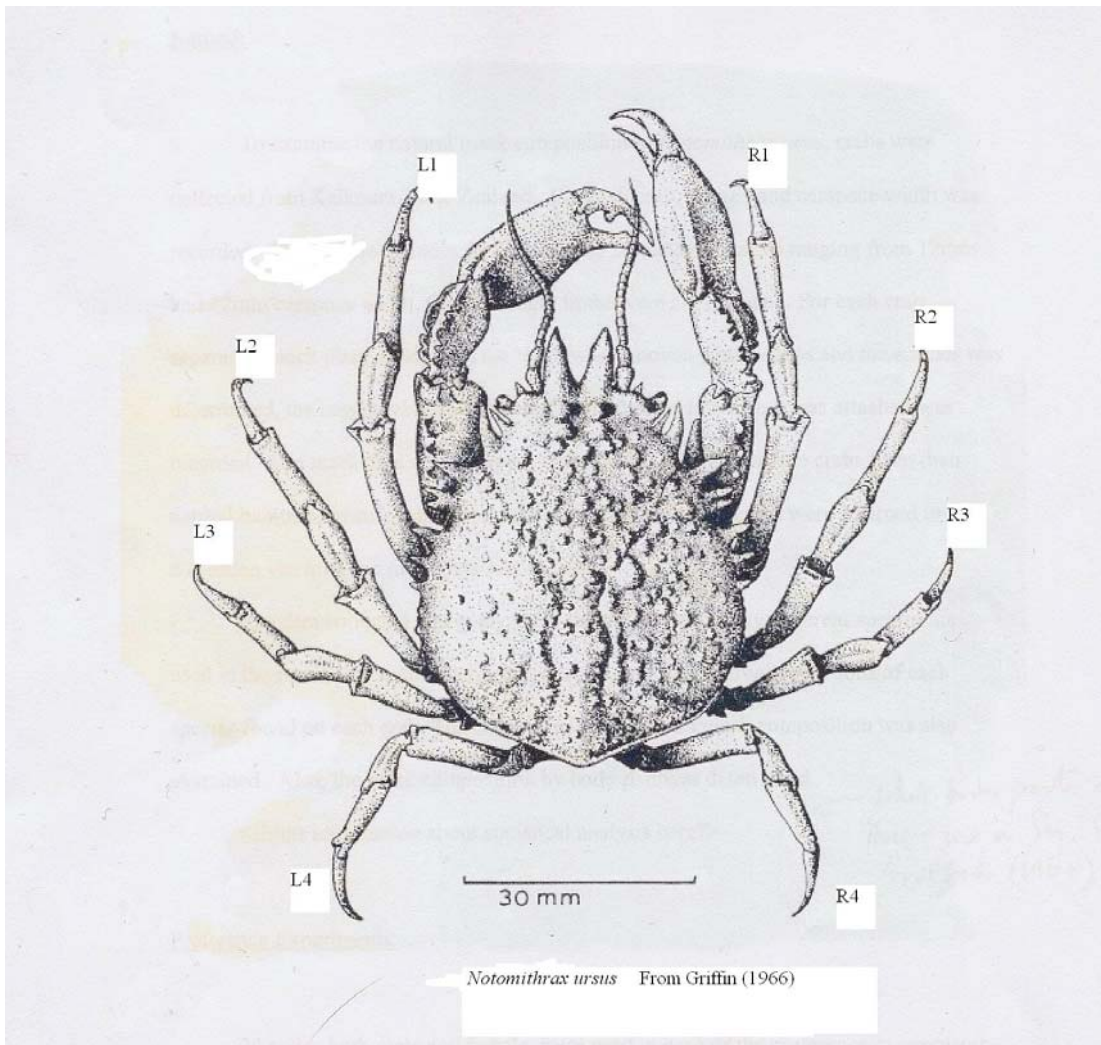
The fact that the crab places algae on its body differently depending on the location, with larger body parts getting more cover, is consistent with the theory that the crab is using the mask as primarily camouflage. The crab placing algae preferentially towards larger body parts increases the chance that it will obscure its entire outline, providing better camouflage than if the mask is evenly placed.

The composition of the mask also varied depending on body part. The percentage of *Euptilota* in the mask was greatest on the carapace and front legs. The percentage shifted to predominantly *Halopteris* on the rear legs. However, the effect was totally accounted for by a change in the amount of *Euptilota* and *Plocamium* by body part. The amount of *Halopteris* in the mask remained constant across the whole body of the crab. The fact that the crab chooses to preferentially put *Euptilota* and *Plocamium* on the carapace may be due to the fact that it is easier to cut larger pieces of those species than *Halopteris*, or because the two red algae grow longer than *Halopteris* does. Also, because of the "fan" structure of these types of algae, they may be best suited to carrying around large amounts because they are lighter while providing the same amount of cover. This may be important when the crab is outside of water. The fan structure may also be important on the carapace because it effectively obscures the chelipeds of the crab, enabling it to eat without giving itself away. Due to the algae pointing anteriorly on the

rostrum, the lower density of the red algae may also be a factor. It is conceivable that the heavier *Halopteris* may impede feeding and movement if it was predominantly in this position, especially out of water.

Diagrams, Graphs and Tables

Figure 2.1: *Notomithrax ursus*.

Notomithrax ursus   From Griffin (1966)

Fig. 2.2 - Percentage of crabs using each species of algae Natural Cover (n = 68)

A bar chart with the y-axis labeled "% of Crabs" ranging from 0 to 100, and the x-axis labeled "Genus of Algae". The bars from left to right are:

- *Euptilota*: 100
- *Halopteris*: 100
- *Plocamium*: ~97
- *Halymenia*: ~46
- *Dasyclonium*: ~43
- *Sertularia (Hydroid)*: ~29
- *Corallina*: ~16
- *Ulva*: ~13
- *Jania*: ~11
- *Ballia*: ~9
- *Others*: ~24
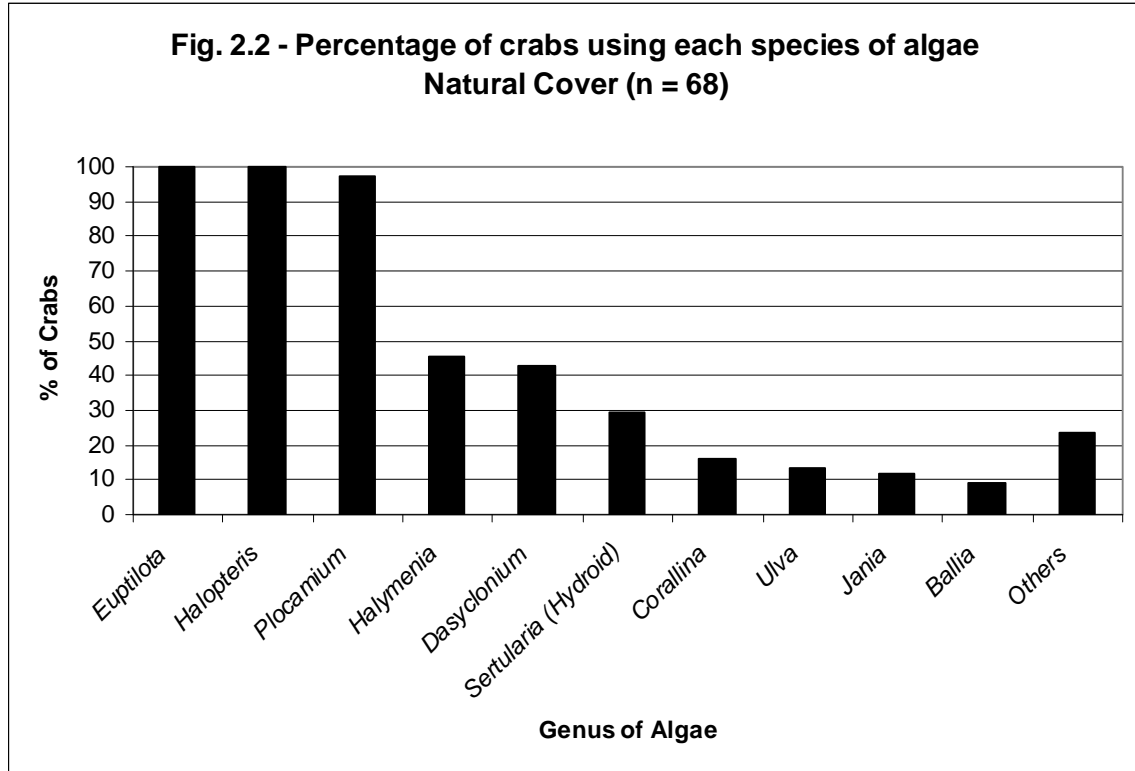
Table 2.1: Percentage mask composition by length and number of pieces

Algae Species	% Length	% Number Pieces
1.) *E. formosissima*	41.1%	36.2%
2.) *H.virgata*	28. 8%	33.0%
3.) *P. microcladioides*	23.3%	22. 8%
Others	6.8%	8.0%

Fig. 2.3 - Pieces of algae vs. Carapace Width
Natural Cover (n =68)

$y = -1.0697x + 74.976$
$R^2 = 0.0545$

$y = -1.0083x + 73.59$
$R^2 = 0.0463$

Fig. 2.4 - Average Length of Algae Pieces vs. Carapace Width
Natural Cover (n = 68)

$y = 0.6731x - 0.4557$
$R^2 = 0.7411$

$y = 0.519x + 2.1384$
$R^2 = 0.7352$

Fig. 2.5 - Change in Species Composition vs. Crab Size
Natural Cover (n = 68)

$y = 0.4118x + 9.7624$
$R^2 = 0.0273$

$y = 0.544x - 0.1559$
$R^2 = 0.0603$

$y = -0.8046x + 36.22$
$R^2 = 0.1925$

Fig. 2.6 - Species Length/Piece vs. Crab Size
Natural Cover (n = 68)

$y = 0.5935x + 0.8138$
$R^2 = 0.365$

$y = 0.668x + 1.4622$
$R^2 = 0.4881$

$y = 0.5209x + 0.5201$
$R^2 = 0.5699$

Table 2.2: Average Total Length (mm) of Algae by Body Part:

L Leg 1	100.9 SD=76.8		R Leg 1	90.1 SD=61.8
L Leg 2	59.9 SD=41.8	Carapace Length = 400.9 (SD = 197.1)	R Leg 2	59.2 SD=38.2
L Leg 3	50.6 SD=39.4		R Leg 3	48.1 SD=34.2
L Leg 4	45.4 SD=34.4		R Leg 4	45.7 SD=32.2

Table 2.3: Average Number of Pieces of Algae by Body Part

L Leg 1	7.0 SD=4.0		R Leg 1	6.6 SD=3.6
L Leg 2	4.7 SD=2.6	Carapace #Pieces = 16.4 SD = 6.8	R Leg 2	4.6 SD=2.6
L Leg 3	4.1 SD=2.3		R Leg 3	4.0 SD=2.4
L Leg 4	3.4 SD=2.4		R Leg 4	3.5 SD=2.1

Fig. 2.7 - Mask Compostion vs. Body Part
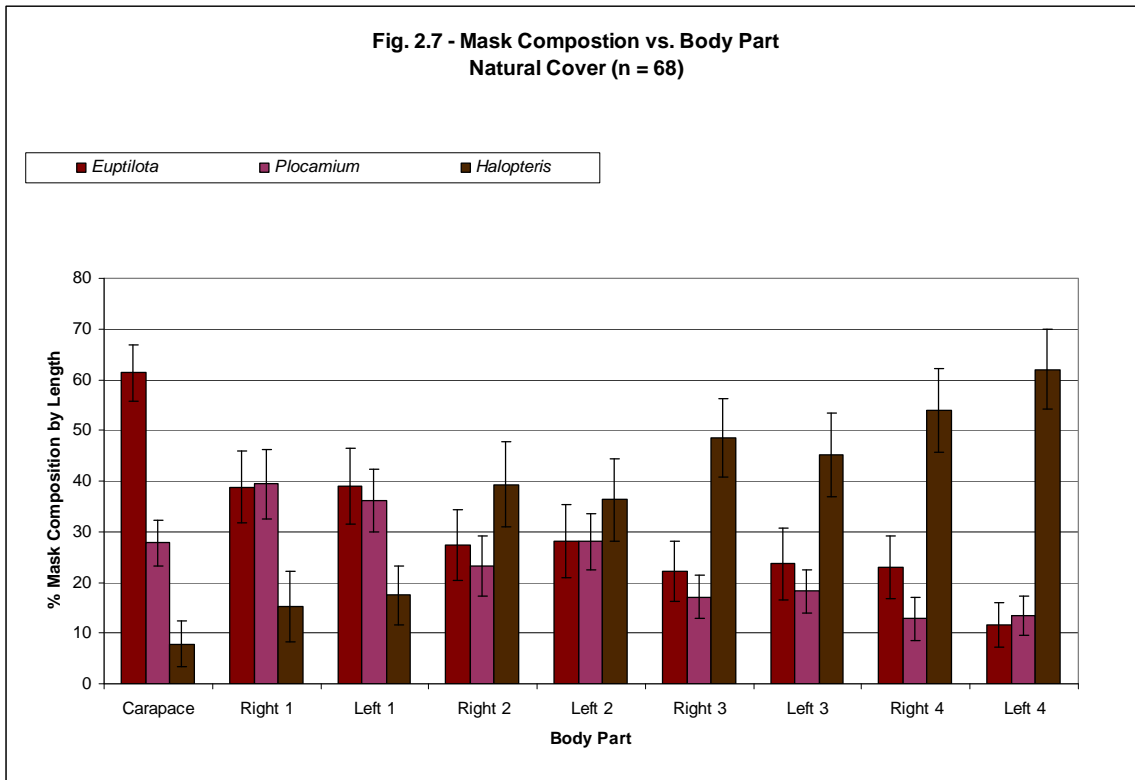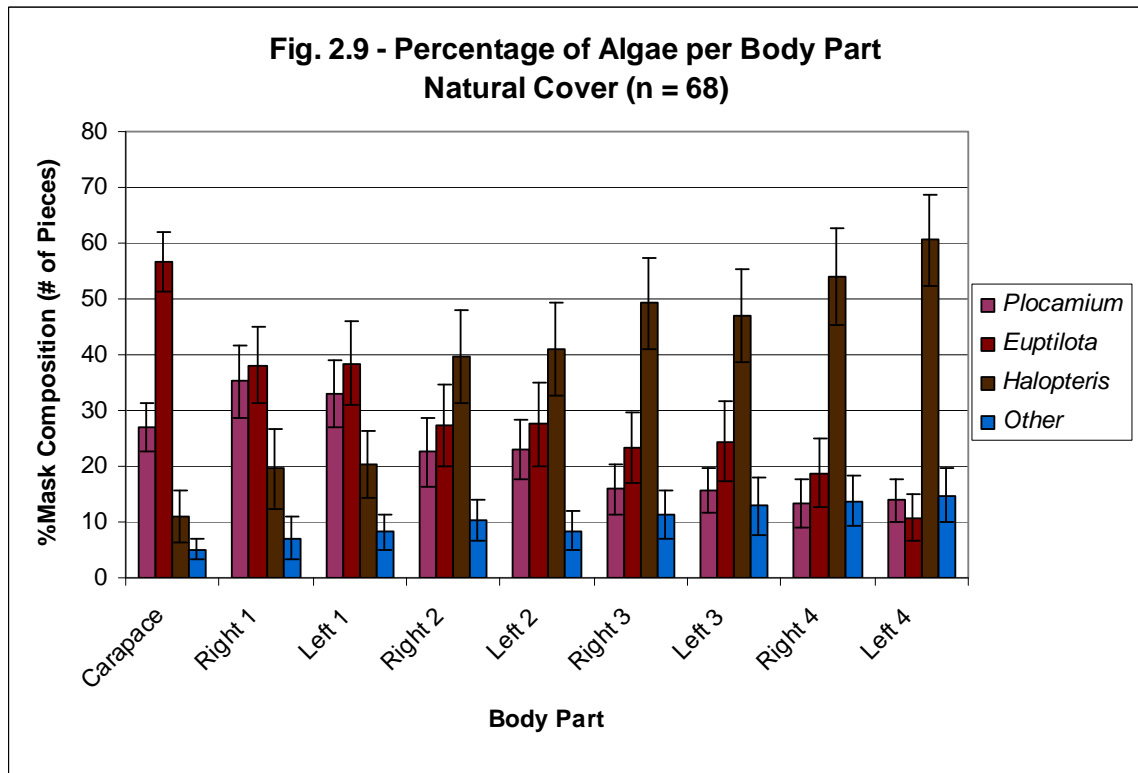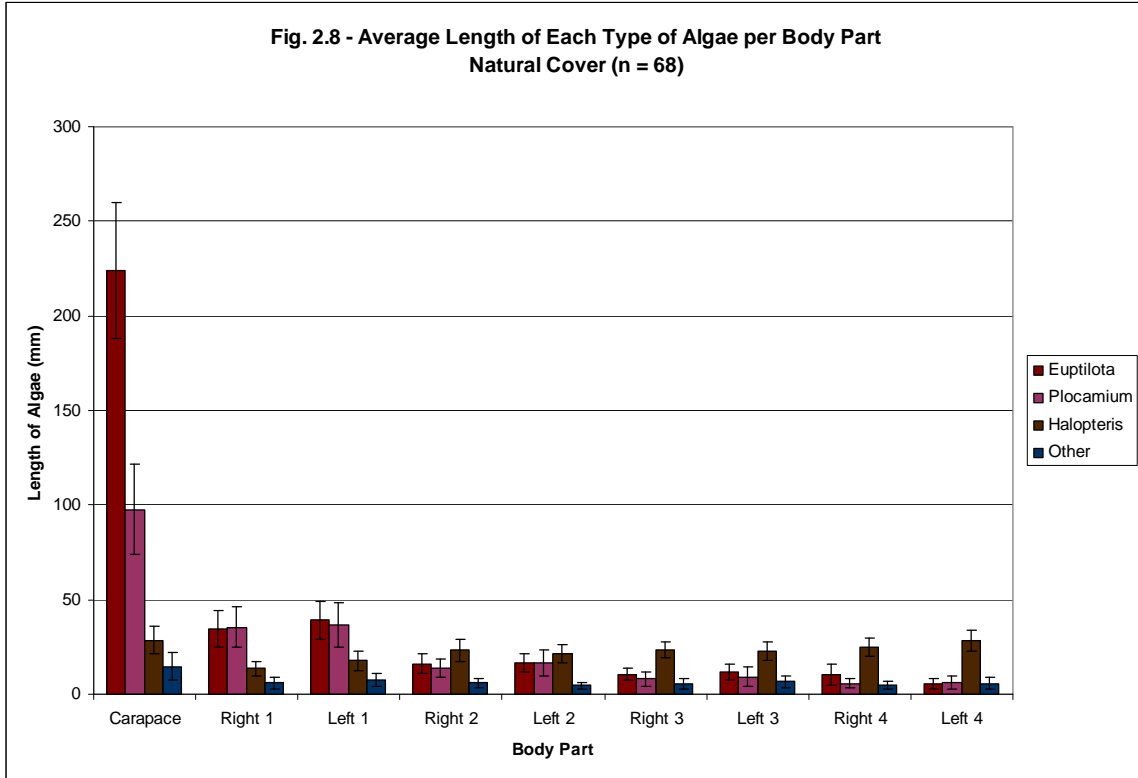Natural Cover (n = 68)

Table 2.4: Percentage of Each Algae Species by Length per Body Part
Natural Cover (n = 68)
E = *Euptilota*
P = *Plocamium*
H = *Halopteris*

L Leg 1	38.9% *E.* 36.2% *P.* 17.5% *H.*			R Leg 1	39.4% *P.* 38.6% *E.* 15.2% *H.*
L Leg 2	36.3% *H.* 28.1% *E.* 28.1% *P.*			R Leg 2	39.3% *H.* 27.4% *E.* 23.2% *P.*
L Leg 3	45.2% *H.* 23.6% *E.* 18.2% *P.*	Carapace 61.4% *Euptilota* 26.8% *Plocamium* 7.9% *Halopteris*		R Leg 3	48.6% *H.* 22.2% *E.* 17.1% *P.*
L Leg 4	62.0% *H.* 13.4% *P.* 11.6% *E.*			R Leg 4	54.0% *H.* 22.9% *E.* 12.8% *P.*

Fig. 2.8 - Average Length of Each Type of Algae per Body Part
Natural Cover (n = 68)

Fig. 2.9 - Percentage of Algae per Body Part
Natural Cover (n = 68)

Fig. 2.10 - Average Number of Pieces of Algae per Body Part
Natural Cover (n = 68)
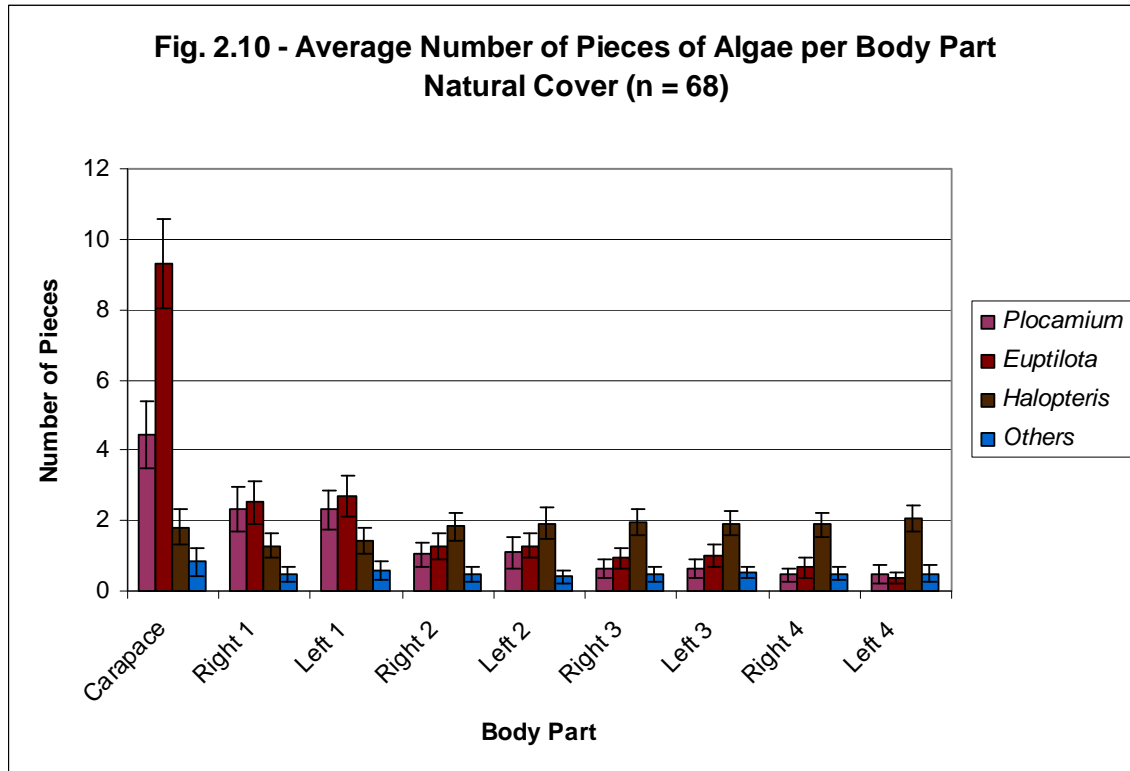
Table 2.5: Percentage of Algae Pieces by Body part
Natural Cover (n = 68)

L Leg 1	38.4% *E.* 33.0% *P.* 20.4% *H.*		R Leg 1	38.1% *E.* 35.3% *P.* 19.5% *H.*
L Leg 2	40.9% *H.* 27.5% *E.* 23.2% *P.*	Carapace 56.9% *Euptilota* 27.1% *Plocamium* 11.0% *Halopteris*	R Leg 2	39.7% *H.* 27.3% *E.* 22.5% *P.*
L Leg 3	47.0% *H.* 24.4% *E.* 15.7% *P.*		R Leg 3	49.3% *H.* 23.3% *E.* 15.9% *P.*
L Leg 4	60.6% *H.* 13.9% *P.* 10.8% *E.*		R Leg 4	54.0% *H.* 18.8% *E.* 13.4% *P.*

Chapter 3: Preference Experiments

Introduction

Contrary to the theory that camouflaging (background matching) behavior is non-selective, there is evidence for crabs having certain preferences for masking material, depending on the purpose of the mask. Strong preferences for certain decoration materials may be linked to many factors including chemical defense (Stachowicz and Hay, 1999), food preferences (Woods and McLay, 1994), handling time (Hultgren et al 2006; Woods and McLay 1994), seasonal variation (Sato and Wada, 2000) or geographic variation (Stachowicz and Hay, 2000) in decoration materials (Hultgren et al 2006).

For example, Cruz-Rivera (2001) found that three species of majid crabs from the Mediterranean coast of Spain (*Macropodia rostrata*, *Acanthonyx lunulatus,* and *Pisa tetrodon*) all showed a degree of specificity in their decoration preferences.

Field and laboratory results conducted by Mastro (1981) showed that the spider crab *Pugettia producta* has a preference for certain types of algae. The crab had different preferences of algae in the wild and in the laboratory which could possibly be explained by the avaiability of certain types in their natural habitat. Also, it was suggested that the difference in species used might be because of the high turbidity of the waters where *P. producta* normally live (Mastro, 1981).

Rorandelli et al (2007) investigated the masking preferences in the spider crab *Inachus phalangium*. They found that there is a preference for algal components that match the background, and especially *Dictyota dichotoma* which is a chemical deterrent

against predators. They also found that the masking patterns vary in different body regions, depending on the functional morphology of the hooked setae.

The spider crab *Lubinia dubia* varies in masking preference depending on geographical factors (Stachowicz and Hay, 2000). Its preferred algae are not found north of North Carolina, however, the crab ranges up to New England. Crabs north of the *Dictyota* range displayed no preference for masking material and just masked to match their background. The southern crabs which did have a strong preference for *Dictyota* switched preferences to the sun sponge *Hymeniacidon heliophila*, which is unpalatable to local fish in the winter and spring when the toxic algae are absent (Stachowicz and Hay, 2000). This geographic shift in preferences may relate to the trend of decreasing total predation and omnivorous consumers in the northern regions. The shifts in predation pressure may account for the different camouflage strategies in the crabs living here (Stachowicz and Hay, 2000).

Algal morphology also may affect masking preferences due to handling time and ease. Some species are larger and tougher than others and more difficult for crabs to manipulate. The aim of this study was to examine the masking preferences of *Notomithrax ursus* in the laboratory. The most common species used in the natural mask and in the environment were given to the crabs to examine if the laboratory preference matched the observed natural preference. The algae species were compared in pairs, first given to the crabs in a 1:1 ratio of each type to test if the relative abundance in the mask matched the abundance in the experimental tanks. Then, the same two algae species were given to the crabs in a 3:1 ratio, to determine if the varying abundance had any effect on

the amount used in the mask. Also, the size of the crab and the location on the body of the algal pieces were examined to examine any effects on preference.

Methods

Thirty crabs, both male and female, were used in each of the preference experiments with moderate carapace widths, approximately between 20 mm and 35 mm. Crabs missing limbs were not included. *Euptilota*, *Halopteris*, *Plocamium* species of algae which are all commonly found in the natural mask composition were used in varying amounts and combinations to test if the crabs have a preference for one more than the others. Also, these commonly used species were compared with *Ulva,* which is uncommonly used in the mask, but very abundant in the crab's natural environment.

Each crab was housed separately and given the choice between two types of algae, either in a 1:1 ratio or a 3:1 ratio. The algae was arranged in clumps held together by clothes pegs and then attached to rocks to secure it in place. Each clump of algae was placed in one corner of the aquarium. For the 1:1 experiments, the same species was placed in opposite diagonals. Each clump contained approximately the same amount of algae and was large enough so that if necessary, the crab would have more than enough algae to fully dress from one clump alone. At the end of each experiment, each corner still contained algae, which shows that at no point did the crab ever run out.

The crabs were left in the experimental tanks until they were "fully dressed" which was determined by ensuring that there was mask material on all body parts. Since the crab normally dresses from front to back, I concluded that they were finished when

the back legs contained mask material. On average it took roughly 4 days for each crab to be fully dressed.

After completely masking, each piece of algae was removed from the crab, identified and measured. Also, the body part on which the piece was found was recorded.

The preference for each type of alga was analyzed by determining the percentage of each type present in the mask by length and by number of pieces. This was also compared by size class of the crab to see if size has any effect on mask preferences. Also, the amount of each species of alga found on each body part was examined.

Results

Euptilota vs. *Halopteris* (1:1 Ratio) Choice Experiment

When given a choice between equal amounts of *Euptilota* and *Halopteris* for the mask, the crabs showed a clear preference for *Euptilota* by number of pieces (χ^2 p < 0.0001) and by total length (t-test, t = 5.768, p < 0.0001). The mask was made up on average of 70.2% *Euptilota* by length and 61.9% *Euptilota* by number of pieces (Table 3.1).

The crabs also showed a preference for *Euptilota* on certain areas of the body. The most *Euptilota* was on the carapace. The amount of *Euptilota* decreased posteriorly on the legs. The percentage of *Euptilota* and *Halopteris* on the mask seemed to change depending on the location of the body part (Figure 3.2). There was a significant difference in the percentage composition of the mask based on body part (ANOVA f =

13.07, p < 0.0001), especially between the carapace and second, third and fourth legs. However, when examining the number of pieces, there was only a significant difference in the amount of *Euptilota* on different body parts (ANOVA f = 54.614, p < 0.0001; Figure 3.1). Even though the percentage of *Halopteris* in the mask increased towards the back of the crab, due to the lessening total number of pieces, the number of pieces of *Halopteris* did not vary significantly across the body of the crab (ANOVA f = 1.50, p = 0.16; Figure 3.1).

There was a correlation between the amount of *Euptilota* used in the mask and crab size by length (r^2 = 0.35; Figure 3.3) and by number of pieces (r^2 = 0.34; Figure 3.4). Similar to the natural mask, the percentage of *Halopteris* decreased with increasing carapace width, so in this experiment, proportionately more *Euptilota* was used.

Euptilota vs. *Halopteris* (1:3 Ratio) Choice Experiment

When the amount of *Halopteris* was increased to 75% of the total available, the amount of *Halopteris* used in the mask almost doubled to 50.4% by length and 56. 8% by number of pieces (Table 3.1). However, this still shows a preference for *Euptilota* (χ^2 p <0.0001), because the expected ratio is 3:1 *Halopteris*: *Euptilota*, but the observed ratio is 1:1.

There was also a clear preference for *Euptilota* by percentage in the mask on the carapace and first legs (ANOVA f = 13.18, p < 0.0001; Figure 3.6). Unlike the 1:1 experiment, there was also a significant difference in the distribution of both types of algae about the body of the crab, when considering the number of actual pieces.

Euptilota varied in amount between the carapace and all legs and between the first legs and second, third and fourth legs (ANOVA f = 45.74, p < 0.001; Figure 3.5). *Halopteris* also varied significantly, but only between the carapace and legs (ANOVA, f = 4.675, p < 0.001; Figure 3.5).

There was a correlation between the percentage of *Euptilota* in the mask and carapace width by length (r^2 = 0.135; Figure 3.7) but not by number of pieces (r^2 = 0.119).

Halopteris vs. *Plocamium* (1:1 Ratio) Choice Experiment

When the crabs were given a choice between *Halopteris* and *Plocamium* in equal proportions, there was no significant difference in the amounts used (χ^2 = 0.66, p = 0.42; Table 3.1). The crabs used 48.5% *Halopteris* pieces in the mask and 42.4% by length, on average.

The percentage of each type of algae used in the mask did vary by body part, with the crabs choosing to preferentially use *Plocamium* on the carapace and front legs and *Halopteris* on the back legs (ANOVA: F = 12.49, p < 0.0001; Figure 3.9). There was a significant variation in the number of pieces of *Plocamium* used on different parts of the body (ANOVA: F = 50.33, p < 0.001; Figure 3.8), but no significant variation in the number of *Halopteris* pieces used across the body (ANOVA: F = 1.233, p = 0.28; Figure 3.8).

There was no correlation between the percentage composition of the mask and carapace width by either total length of the algae ($r^2 = 0.12$) or number of pieces ($r^2 = 0.072$).

Halopteris vs. *Plocamium* (3:1 Ratio) Choice Experiment

When the proportion of *Halopteris* in the experimental tanks was increased to 75%, the amount of *Halopteris* used in the mask only increased marginally – to 49.29% of the total length of algae and 55.22% of the total number of algae pieces. This preference for *Plocamium* was significant (χ^2 p < 0.0001; Table 3.1).

There was a significant difference in the percentage of *Plocamium* in the mask across the body (ANOVA f = 13.57, p < 0.0001; Figure 3.11). The carapace and the first legs had similar percentages of *Plocamium*, but differed significantly from the rest of the legs. Examining the number of actual pieces of algae in the mask, there was a significantly greater amount of *Plocamium* on the carapace and first legs than on the last three legs (ANOVA f = 31.08, p < 0.0001; Figure 3.10). The number of pieces of *Halopteris* in the mask was also significantly greater, between the carapace and first legs, but not between any other part of the body (ANOVA f = 3.136, p = 0.002; Figure 3.10).

There was no significant correlation between the percentage composition of the mask by length versus crab size ($r^2 = 0.090$) or by percentage of the number of total pieces ($r^2 = 0.054$).

Halopteris vs. *Ulva* (1:1 Ratio) Choice Experiment

When, the crabs were given an equal amount of *Halopteris* and *Ulva*, they showed a very clear preference for *Halopteris* ($p < 0.0001$, Table 3.1). *Ulva* only made up 6.5% of the mask by length and 6. 9% of the mask by number of pieces (Table 3.1).

The percent algal composition of the mask did not vary significantly depending on the location on the body (ANOVA: $F = 0.96$, $p = 0.47$; Figure 3.13). Both *Halopteris* and *Ulva* showed significant variation of the distribution on the body by number of pieces. Both species of algae were more abundant on the carapace than the legs. (ANOVA of *Halopteris:* $F = 28.8$, $p < 0.001$; ANOVA of *Ulva:* $F = 2.74$, $p = 0.007$; Figure 3.12).

The percent composition of the mask was correlated significantly with the carapace width of the crabs. The percentage of *Halopteris* in the mask decreased by total length ($r^2 = 0.14$; Figure 3.14) and total number of pieces ($r^2 = 0.199$; Figure 3.15).

Halopteris vs. *Ulva* (1:3 Ratio) Choice Experiment

When the amount of *Ulva* in the experiment was increased to three times the amount of *Halopteris*, the crabs still showed a clear preference for *Halopteris*, although the percentage of *Ulva* used did increase a small amount. The crabs used 15.69% *Ulva* by length and 15.9% *Ulva* by number of pieces (χ^2 $p < 0.0001$; Table 3.1).

The mask composition was evenly spread across the body of the crab (ANOVA: $F = 0.89$, $p = 0.53$; Figure 3.17). However, the number of pieces of both species of algae

varied significantly by body part of the crab. There was a significantly different amount of *Halopteris* on the carapace of the crab than on any of the legs, and also a significant difference between the first pair of legs and the last pair (ANOVA f = 43.375, p < 0.0001; Figure 3.16). *Ulva* also varied significantly between the carapace of the crab and the last 3 pairs of legs (ANOVA f = 5.798, p < 0.0001; Figure 3.16).

There was no significant correlation between the percentage of *Halopteris* in the mask and the carapace width of the crabs for either length (r^2 < 0.0001) or number of pieces (r^2 = 0.0038).

Euptilota vs. *Ulva* (1:1 Ratio) Choice Experiment

When the crabs were given a choice between *Euptilota* and *Ulva* in equal amounts, there was a very strong preference for *Euptilota*. *Ulva* made up, on average, only 6.9% of the mask by length of algae and 10.4% of the mask by number of pieces (χ^2 p < 0.0001; Table 3.1).

There was no significant difference in the percentage of *Ulva* used across the body of the crab (ANOVA f = 1.767, p = 0.084; Figure 3.19). There was a significantly larger number of pieces of *Euptilota* used on the carapace of the crab when compared with all of the legs and also significantly more pieces of *Euptilota* between the first legs and last legs (ANOVA f = 56.04, p < 0.0001; Figure 3.18). However, there was no significant difference between any of the body parts in terms of number of *Ulva* pieces used (ANOVA f = 0.97, p = 0.46; Figure 3.18).

There was no correlation between the percentage of *Ulva* used in the mask and carapace width, either by number of pieces ($r^2 = 0.0006$) or length ($r^2 = 0.021$).

Euptilota vs. *Ulva* (1:3 Ratio) Choice Experiment

The amount of *Ulva* used in the mask increased a small amount when the crabs were given three times as much *Ulva* in the experimental tanks. They used 9.2% *Ulva* by length and 12.8% by number of pieces (Table 3.1). There was still a very strong preference for *Euptilota* as the mask material (χ^2 p < 0.0001).

The percentage of *Ulva* in the mask remained relatively the same across the crab's body (ANOVA: F = 1.90, p = 0.06; Figure 3.21). There was no significant difference in the number of pieces of *Ulva* on different parts of the crab (ANOVA: F = 1.04, p = 0.40; Figure 3.20). The varying amounts of total pieces of algae on different body parts of the crab was accounted for entirely by *Euptilota*. There was a significant difference in the numbers of pieces of *Euptilota* between the carapace and all legs, and also between the first legs and last two pairs (ANOVA: F = 76.1, p < 0.0001).

There was no significant correlation between the percentage of *Ulva* used in the mask and carapace width either by number of pieces ($r^2 = 0.008$) or length ($r^2 = 0.002$).

Euptilota vs. _Plocamium_ (1:1 Ratio) Choice Experiment

When given equal amounts of _Plocamium_ and _Euptilota_, the crabs showed no significant preference for one species over the other (χ^2 p = 0.13). The crabs used 56.0% _Euptilota_ by length and 51.2% _Euptilota_ by number of pieces (Table 3.1).

The composition of the mask by percentage number of pieces did not vary significantly depending on the body part of the crab. The proportions of _Euptilota_ and _Plocamium_ in the mask were approximately the same on all body parts (ANOVA: F = 1.80, p = 0.08; Figure 3.23). The number of pieces of each species of algae did vary significantly depending on location. For _Euptilota_, the number of pieces on the carapace was significantly greater than on all of the legs and the number of pieces on the first pair of legs was significantly greater than on the last pair of legs (ANOVA: F = 37.6, p < 0.0001; Figure 3.22). For _Plocamium_, the number of pieces on the carapace was significantly greater than all legs and the number of pieces on the first pair of legs was significantly greater than on the other 3 pairs of legs (ANOVA: F = 24.9, p < 0.0001; Figure 3.22).

The composition of the mask was not correlated with the size of the crab. The percentage of _Euptilota_ in the mask by length (r^2 = 0.088) or by number of pieces (r^2 = 0.101) did not vary depending on carapace width of the crabs.

Euptilota vs. *Plocamium* (3:1 Ratio) Choice Experiment

When the amount of *Euptilota* given to the crabs was increased to 75% of total, the crabs showed a preference for *Plocamium* (χ^2 p < 0.0001). The crabs used 68.9 % *Euptilota* by length and 62.2% *Euptilota* by number of pieces (Table 3.1).

The percentages of each species in the mask remained constant on the entire body of the crab (ANOVA: F = 1.41, p = 0.193; Figure 3.25). The actual number of pieces of each species did vary significantly across different body parts. For *Plocamium*, the number of pieces on the carapace was significantly greater than the number of pieces on the last three pairs of legs and the number of pieces on the first pair of legs was significantly greater than on the last pair of legs (ANOVA: F = 10.4, p < 0.0001; Figure 3.24). For *Euptilota*, the number of pieces on the carapace was significantly greater than the number of pieces on any of the legs and the number of pieces on the first pair of legs was significantly greater than on the last pair of legs (ANOVA: F = 53.1, p < 0.0001; Figure 3.24).

There was no significant correlation between the mask composition and carapace width for either length (r^2 < 0.001) or number of pieces (r^2 < 0.0001).

Discussion

<u>*Euptilota* vs. *Halopteris* Choice Experiments</u>

When given a choice between *Euptilota* and *Halopteris* in equal amounts, *N. ursus* showed a clear preference for *Euptilota* since this species made up ~62% of the mask pieces on average, compared to the expected 50% if crabs chose based on their background alone.

The distribution of *Euptilota* and *Halopteris* in the mask differed based on the location on the body of the crab. Similar to what we see in the species distribution of the natural mask, the amount of *Euptilota* in the mask was greatest on the carapace and front legs of the crab, and decreasing towards the back. The amount of *Halopteris*, like in the natural mask, stayed constant across the entire body.

There was a decrease in the percentage of *Halopteris* used in the mask with increasing crab size. This is consistent with what we see in the wild caught *N. ursus*. Perhaps this is because larger pieces of *Euptilota* are easier to cut than *Halopteris*, or because the branching red algae provide more cover for the same length piece.

When the amount of *Halopteris* that was given to the crabs was increased to 75% of the total, the amount of *Halopteris* used in the mask also increased to ~57%. However, there was still a clear preference for *Euptilota*, since if the crab was randomly selecting pieces based on availability, we would expect *Halopteris* to make up 75% of the mask.

The crabs continued to show a preference towards putting *Halopteris* on the last three pairs of legs. The distribution pattern was the same as I saw in the 1:1 experiment and in the natural mask – with *Euptilota* preferentially placed on the carapace and first legs of the crab, and decreasing posteriorly. Even though all body parts contained more *Halopteris* in the 1:3 experiment than in the 1:1 experiment, the second and third legs received a greater increase than the carapace or first pair of legs.

For this experiment, there was a significant increase in the percentage of *Euptilota* by length used in the mask and a small (but not significant) increase in the percentage number of pieces with increasing carapace width.

Halopteris vs. *Plocamium* Choice Experiments

When given a choice between the two species of algae in equal proportions, *N ursus* showed no clear preference for one over the other. The percentage of *Plocamium* in the mask was ~51%. However when the algae in the experimental tanks consisted of 75% *Halopteris*, the percentage of *Plocamium* used only decreased to ~45%. If the crab was choosing based on background abundance alone, the percentage of *Plocamium* in the mask should have been 25%.

This discrepancy in the apparent algal preferences of the crab may be explained by the mask distribution on the body. The crab may prefer to keep a certain amount of *Plocamium* on the carapace and front legs and use *Halopteris* as filler. This hypothesis is consistent with the results. You can see by comparing the two graphs of the number of

pieces of each species (Figures 3.8, 3.10) that the number of pieces of *Plocamium* used on each area remains relatively the same between the two experiments.

Like we see in the wild and similar to *Euptilota*, the crab chooses to place *Plocamium* on its carapace and front legs, with decreasing amounts towards the back. Also like the natural mask distribution, in both experiments the overall distribution of *Halopteris* stays relatively constant across the entire body.

Halopteris vs. *Ulva* Choice Experiments

In the experiment in which the background contained 50% *Ulva*, *Notomithrax ursus* showed a very strong preference for *Halopteris*. Only ~7% of the mask on average consisted of *Ulva*. When the amount of *Ulva* given to the crabs was increased to 75%, the amount used in the mask increased to ~16%. However, there was still a very strong preference for *Halopteris*. If the crab was only choosing based on availability, we would expect the percentage of *Ulva* in the mask to be much higher. This result is consistent with the natural data. *Ulva* is only rarely used in the mask despite it being one of the most common species in the crab's habitat.

In both experiments, the relative proportions of each species remained constant across the entire body of the crab, showing that for these two species, there is no preference based on body part. In addition, when examining the number of pieces of each type of algae, they both are more abundant on the carapace of the crab, which is consistent with the fact that the total number of pieces of algae in the mask is usually greater on the carapace.

Similar to what was seen in the *Halopteris* vs. *Plocamium* experiments, the number of pieces of *Halopteris* remained relatively constant across the whole body of the crab. When extra *Ulva* was given, the crabs put on more pieces, while keeping the actual number of *Halopteris* pieces constant. This may show that the crab actively seeks out *Halopteris* to use in the mask, but will use other, less preferred species (like *Ulva*) if it comes across them.

There was a significant decrease in the percentage of *Halopteris* used in the mask with increasing carapace width. This could be evidence that *Ulva* isn't preferred because it is too hard to handle. It stands to reason that larger crabs may be better equipped to deal with a thallose alga like *Ulva* more efficiently than smaller crabs because of their larger, stronger chelipeds.

Euptilota vs. *Ulva* Choice Experiments

When given equal amounts of *Ulva* and *Euptilota*, *N. ursus* only used on average ~10% *Ulva* in the mask. When the amount of *Ulva* was increased to 75%, the amount of *Ulva* used only increased to ~13%. This shows a very strong preference for *Euptilota* against *Ulva*. Again, this is consistent with what is seen in the natural mask composition. *Ulva*, despite being one of the most common species of algae present in the crabs habitat, is only very rarely used.

The percentage of *Ulva* varied across the body of *N.ursus*, with very little present on the carapace and more towards the rear legs of the crab. This result was shown for both experiments. Also, for both experiments, the number of pieces of *Euptilota* on the

carapace was significantly greater than on the legs. The number of pieces of *Ulva* was constant across the body of the crab. Again, this may be evidence that the crab actively seeks out *Euptilota* to use in the mask, but will use alternate species if available and are indiscriminate about their placement on the body.

Euptilota vs. *Plocamium* Choice Experiments

There was no significant preference between *Euptilota* and *Plocamium* when they were given equal amounts. *Plocamium* made up, on average, ~49% of the mask material. However, when the crabs were given 75% *Euptilota* and 25% *Plocamium*, the amount of *Plocamium* decreased, but not as much as would be expected if the algae choice was based on availability alone. In the 1:3 *Polcamium*: *Euptilota* experiment, *Plocamium* contributed ~38% of the mask pieces. This result is similar to what was seen in the *Halopteris* vs. *Plocamium* choice experiments.

However, this time, there is no constant number of pieces of *Plocamium* present in the mask of both experiments. Especially on the carapace, the number of pieces of *Euptilota* in the mask increases when *Euptilota* is more abundant and the number of pieces of *Plocamium* decrease. In both experiments the number of pieces of each species varied significantly depending on the body part. Both species were more abundant on the carapace and front legs and decreased towards the back.

Tables and Graphs

Table 3.1: Summary: Average % Algae Species use in the mask for each preference experiment.

Experiment	% Length	% Piece	
Euptilota : Halopteris 1:1	70.3% E 29.7% H	61.9% E 38.1 % H	χ^2 p< 0.0001
Euptilota : Halopteris 1:3	49.6% E 50.4% H	43.2% E 56.8% H	χ^2 p< 0.0001
Plocamium : Halopteris 1:1	42.4%H 57.7% P	48.5% H 51.5% P	χ^2 p = 0.418
Plocamium : Halopteris 1:3	49.3% H 50.7% P	55.2%H 44.8%P	χ^2 p < 0.0001
Halopteris : Ulva 1:1	93.5% H 6.5% U	93.1% H 6.9% U	χ^2 p < 0.0001
Halopteris : Ulva 1:3	84.3% H 15.7% U	84.1%H 15.9%U	χ^2 p< 0.0001
Euptilota : Ulva 1:1	93.1% E 6.9% U	89.6% E 10.4% U	χ^2 p < 0.0001
Euptilota : Ulva 1:3	90.8% E 9.2% U	87.3% E 12.8% U	χ^2 p< 0.0001
Euptilota : Plocamium 1:1	56.0% E 44.0% P	51.2% E 48.8% P	χ^2 p = 0.13
Euptilota : Plocamium 3:1	68.0% E 31.1% P	62.2% E 37.8% P	χ^2 p < 0.0001

Figure 3.1 - Number of Pieces per Body Part
Euptilota vs. *Halopteris* (1:1 Ratio) Choice Experiment (n = 30)
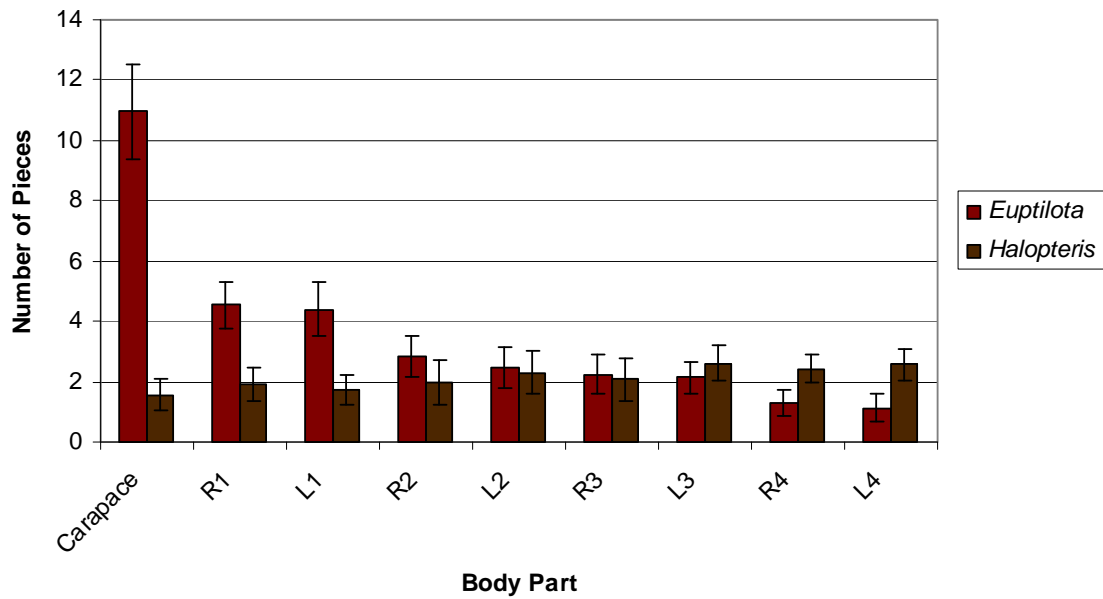
Figure 3.2 - Percentage Number of Pieces by Body Part
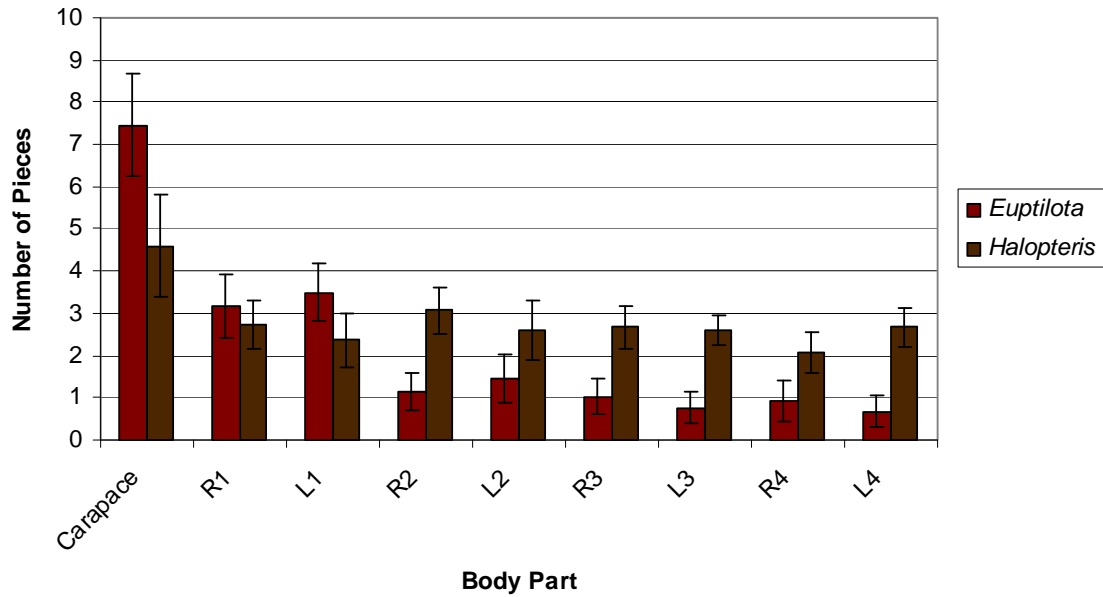*Euptilota* vs *Halopteris* (1:1 Ratio) Choice Experiment (n = 30)
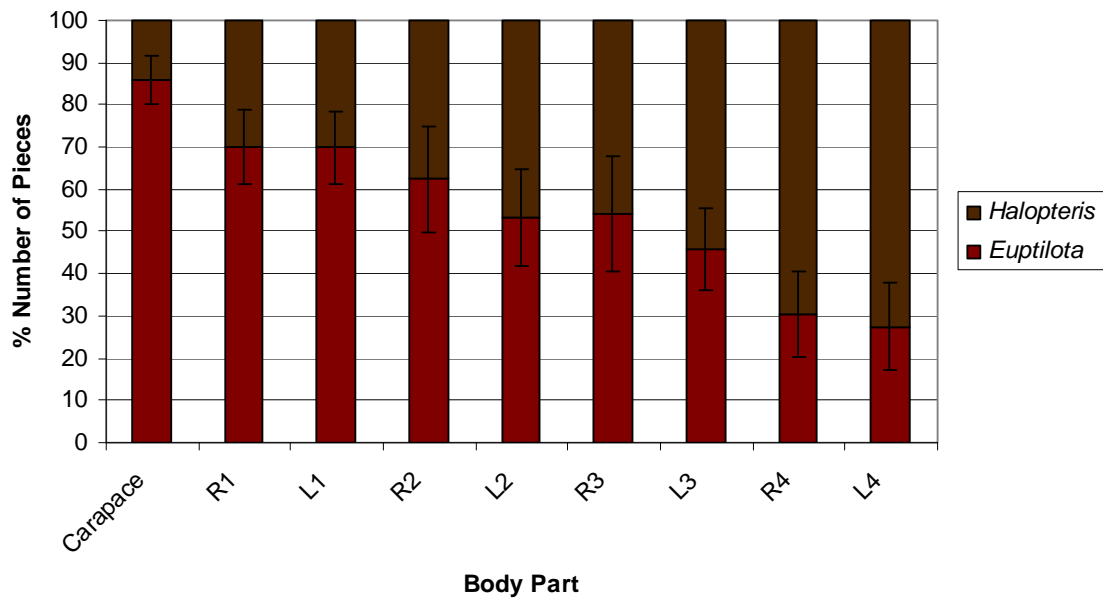
Figure 3.3 - Percentage *Euptilota* Length vs. Crab Size
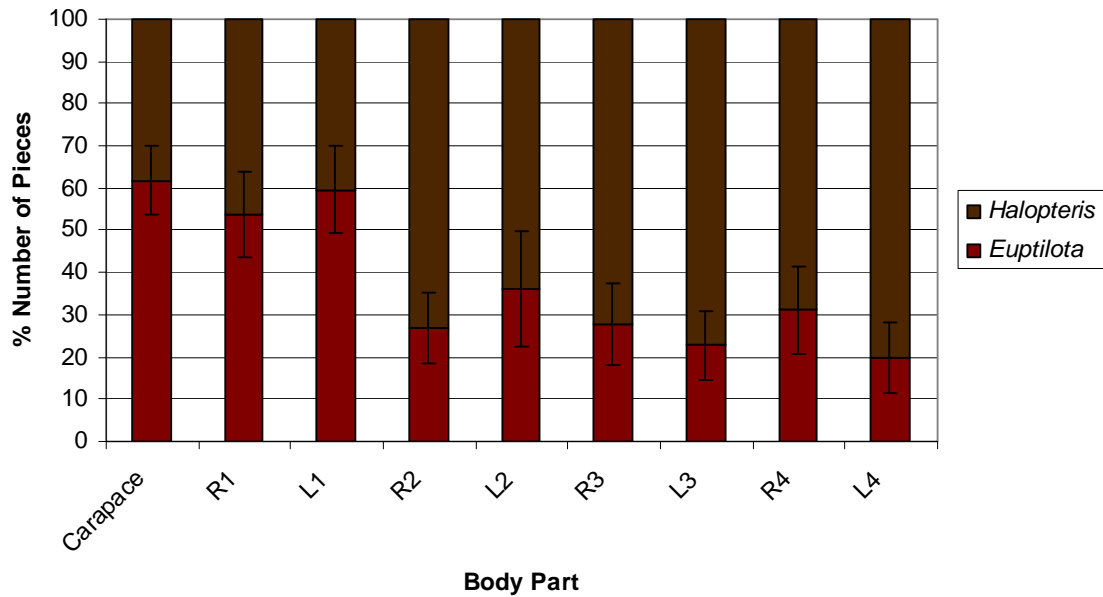***Euptilota* vs. *Halopteris* (1:1 Ratio) Choice Experiment (n = 30)**

$y = 2.3545x + 7.8343$
$R^2 = 0.3485$
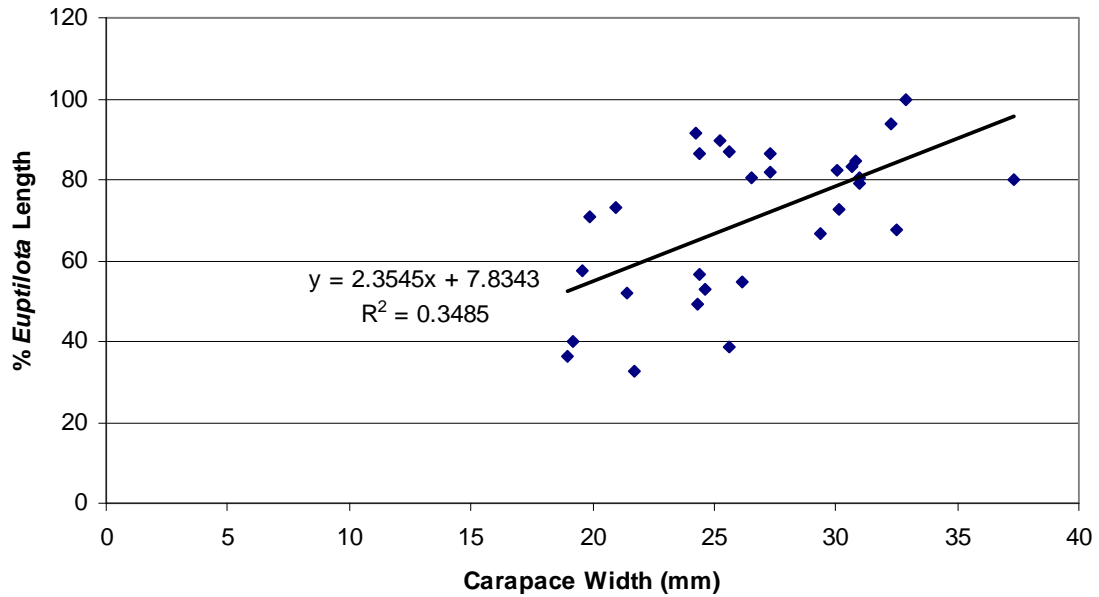
Figure 3.4 - Percentage *Euptilota* by # of Pieces vs. Crab Size
Euptilota vs. Halopteris (1:1 Ratio) Choice Experiment (n = 30)

$y = 2.3427x - 0.2241$
$R^2 = 0.3362$

57
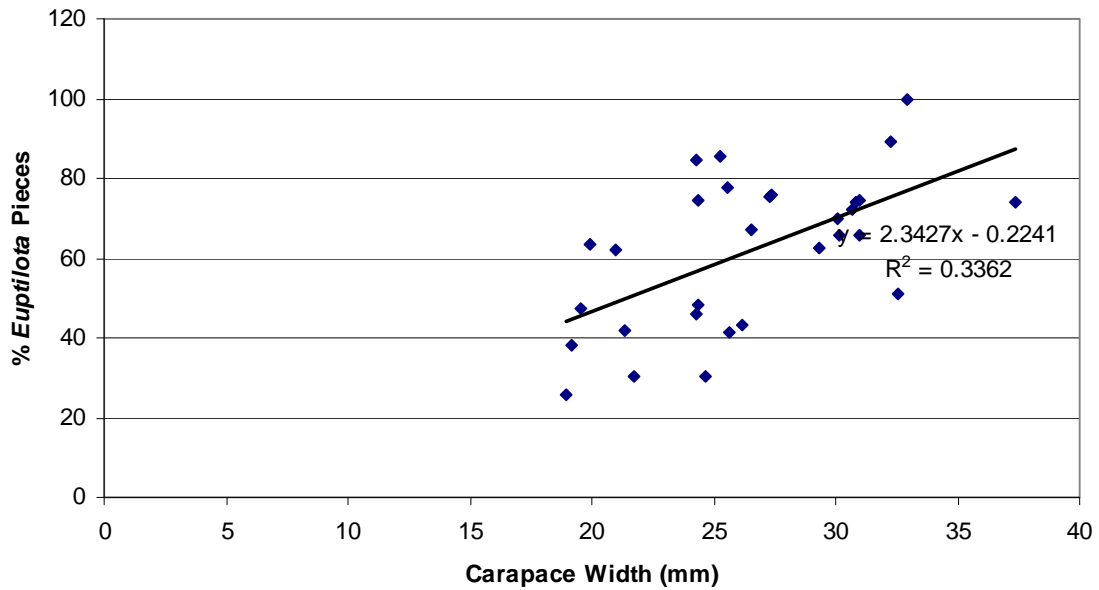
Figure 3.5 - Average Number of Pieces per Body Part
***Euptilota* vs. *Halopteris* (1:3 Ratio) Choice Experiment (n = 30)**

Figure 3.6 - Number of Pieces by Body Part
***Euptilota* vs. *Halopteris* (1:3 Ratio) Choice Experiment (n = 30)**

Figure 3.7 - Percentage *Euptilota* by Length vs. Crab Size
Euptilota vs .*Halopteris* (1:3 Ratio) Choice Experiment (n = 30)

$y = 1.4578x + 11.544$
$R^2 = 0.1349$

% *Euptilota* Length

Carapace Width (mm)
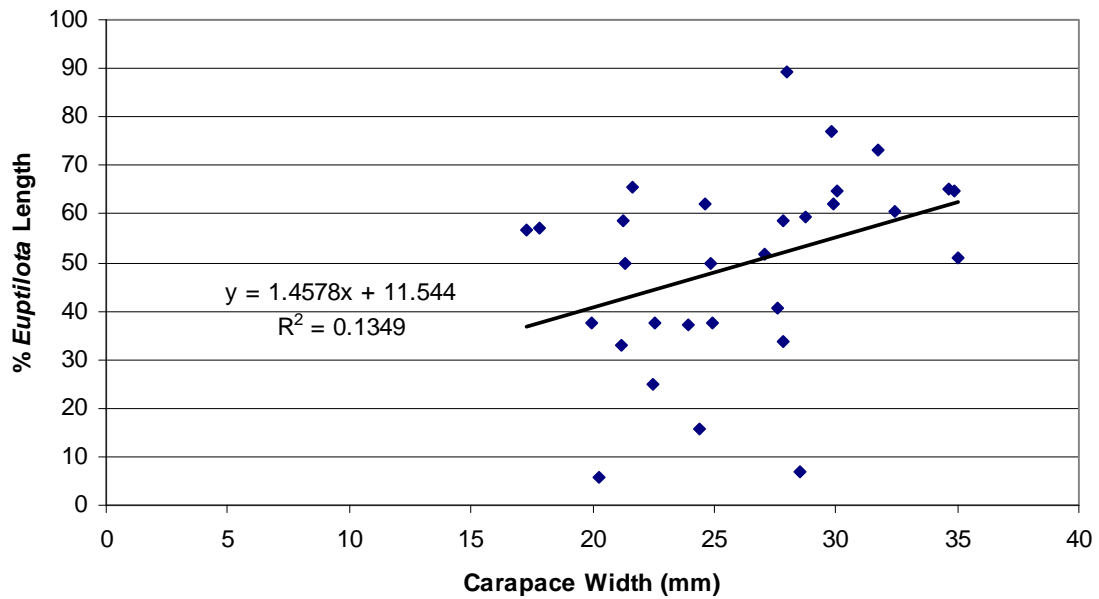
Figure 3.8 - Average Number of Pieces per Body Part
**_Halopteris_ vs. _Plocamium_ (1:1 Ratio) Choice Experiment (n= 29)**

Number of Pieces

Body Part

Plocamium
Halopteris
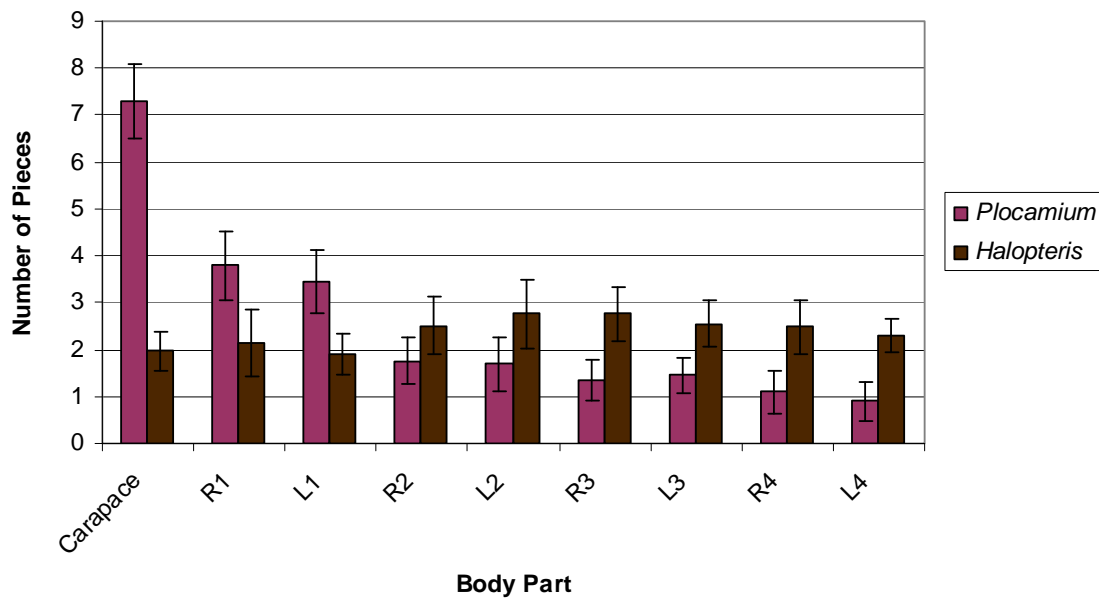
Figure 3.9 - Percentage Number of Pieces by Body Part
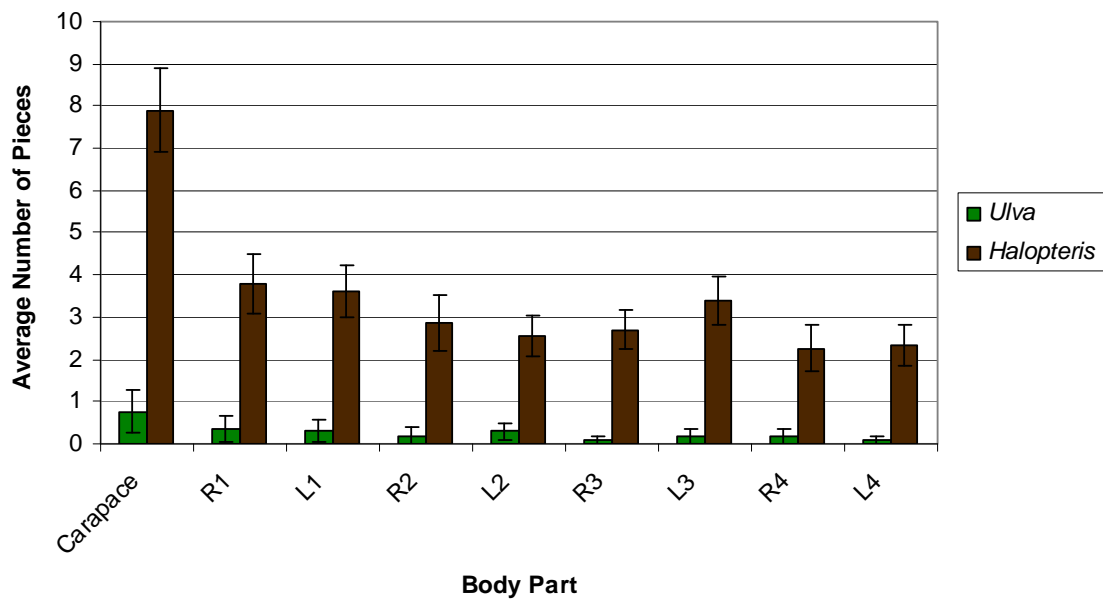*Halopteris* vs *Plocamium* (1:1 Ratio) Choice Experiment (n =29)
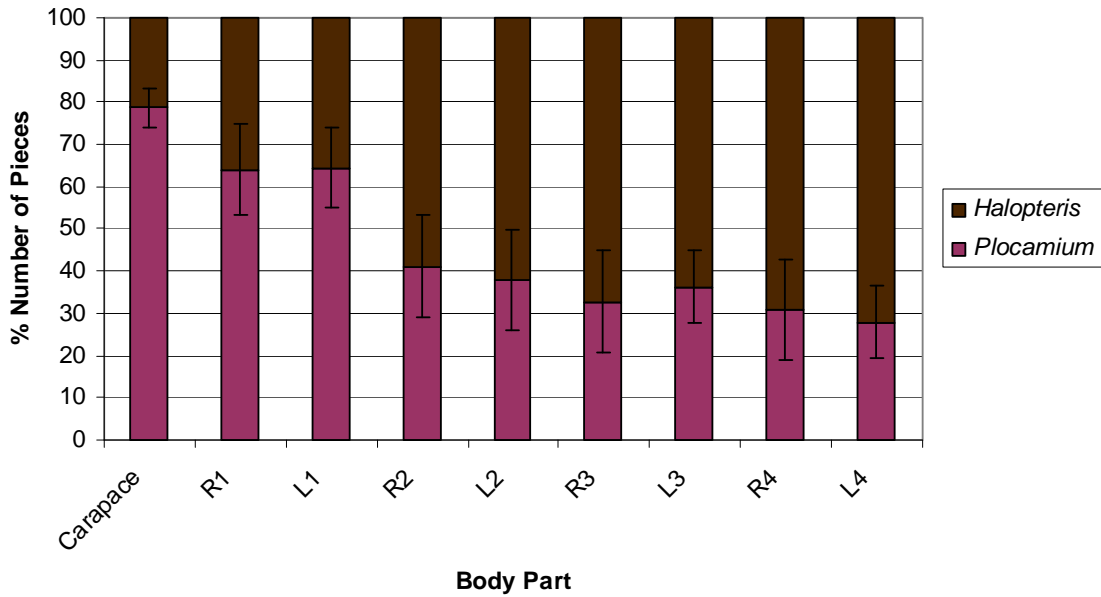
Figure 3.10- Average Number of Pieces per Body Part
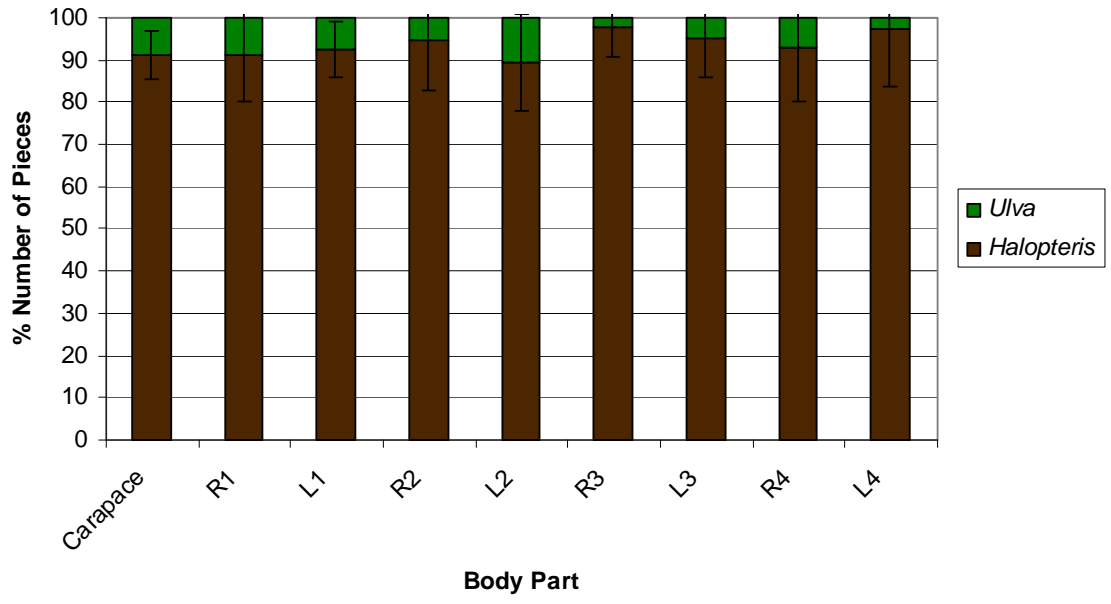**Halopteris vs. Plocamium (3:1 Ratio) Choice Experiment (n =29)**
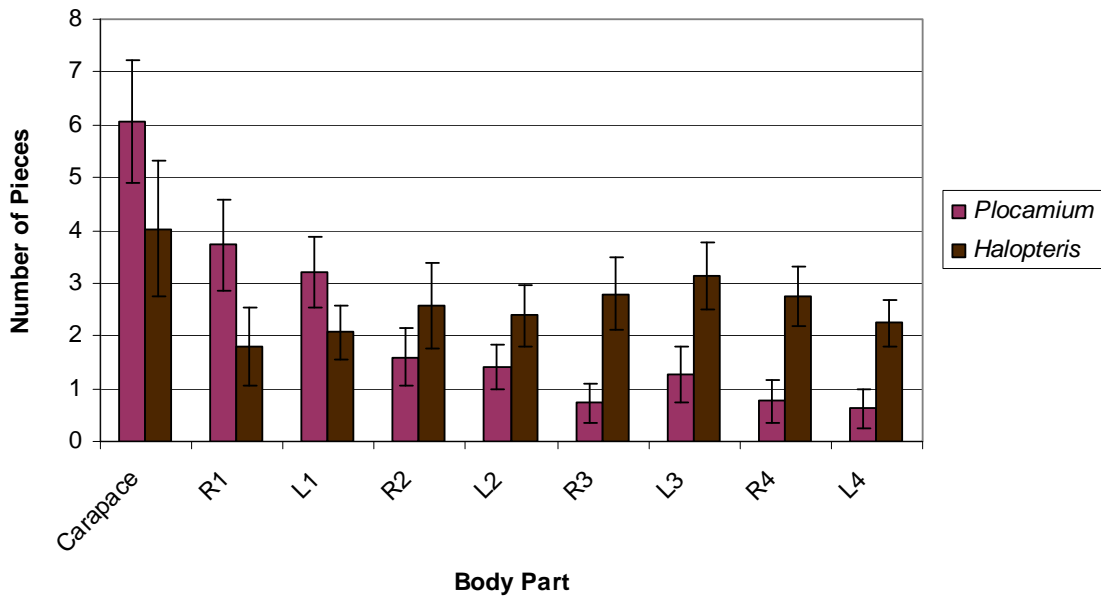
Figure 3.11 - Percentage Number of Pieces by Body Part
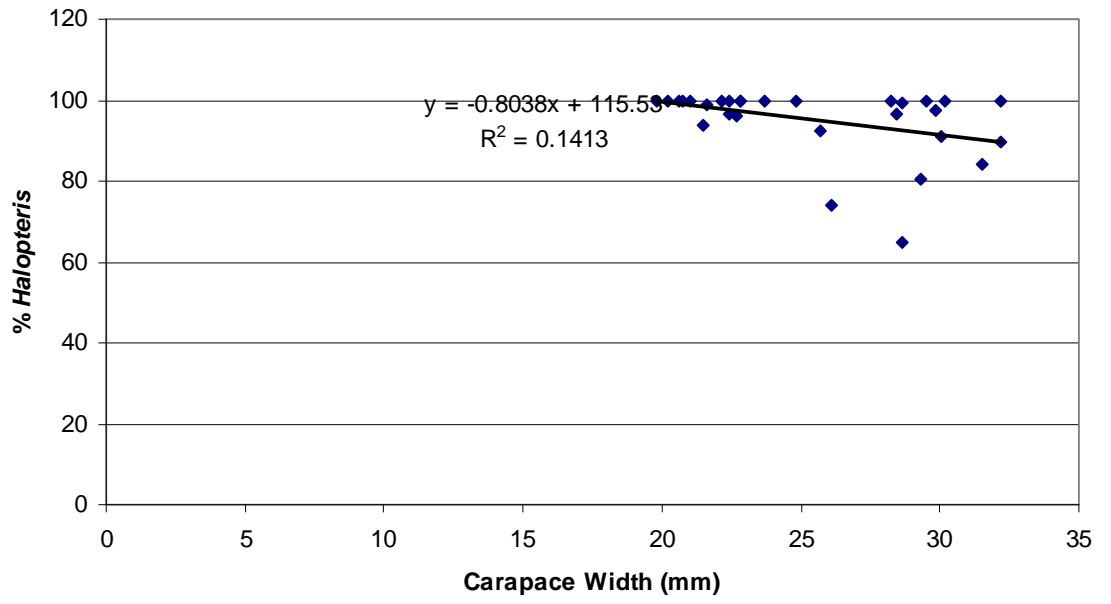*Plocamium* vs. *Halopteris* (1:3 Ratio) Choice Experiment
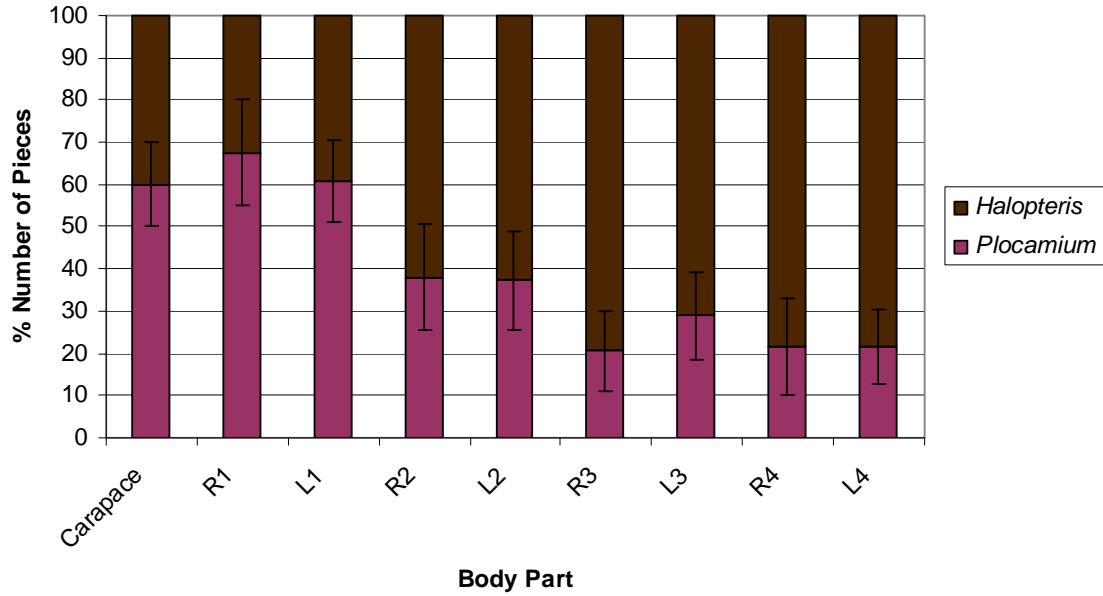
Figure 3.12 - Average Number of Pieces per Body Part
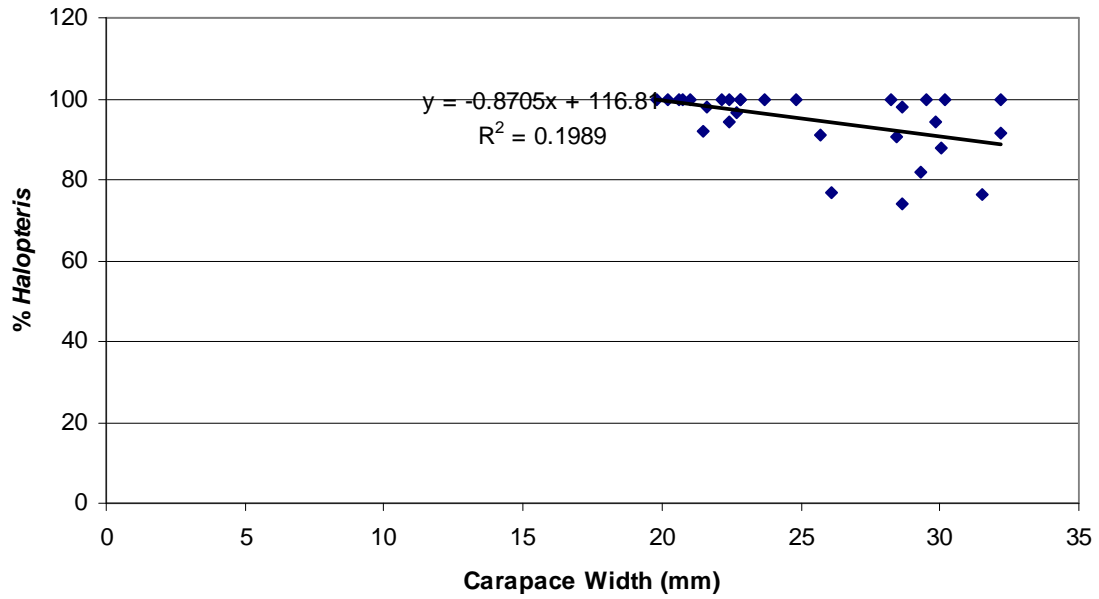*Halopteris* vs. *Ulva* (1:1 Ratio) Choice Experiment (n = 30)

Figure 3.13 - Percentage Number of Pieces by Body Part
Halopteris vs *Ulva* (1:1 Ratio) Choice Experiment (n = 30)

Figure 3.14 - Percentage *Halopteris* by Length vs. Crab Size
Halopteris vs. *Ulva* (1:1 Ratio) Choice Experiment (n = 30)

$y = -0.8038x + 115.53$
$R^2 = 0.1413$

Figure 3.15 - Percentage *Halopteris* Pieces vs. Crab Size
***Halopteris* vs. *Ulva* (1:1 Ratio) Choice Experiment (n = 30)**

$y = -0.8705x + 116.8$
$R^2 = 0.1989$

Figure 3.16 - Average Number of Pieces per Body Part
***Halopteris* vs. *Ulva* (1:3 Ratio) Choice Experiment (n = 30)**

Figure 3.17 - Percentage Number of Pieces by Body Part
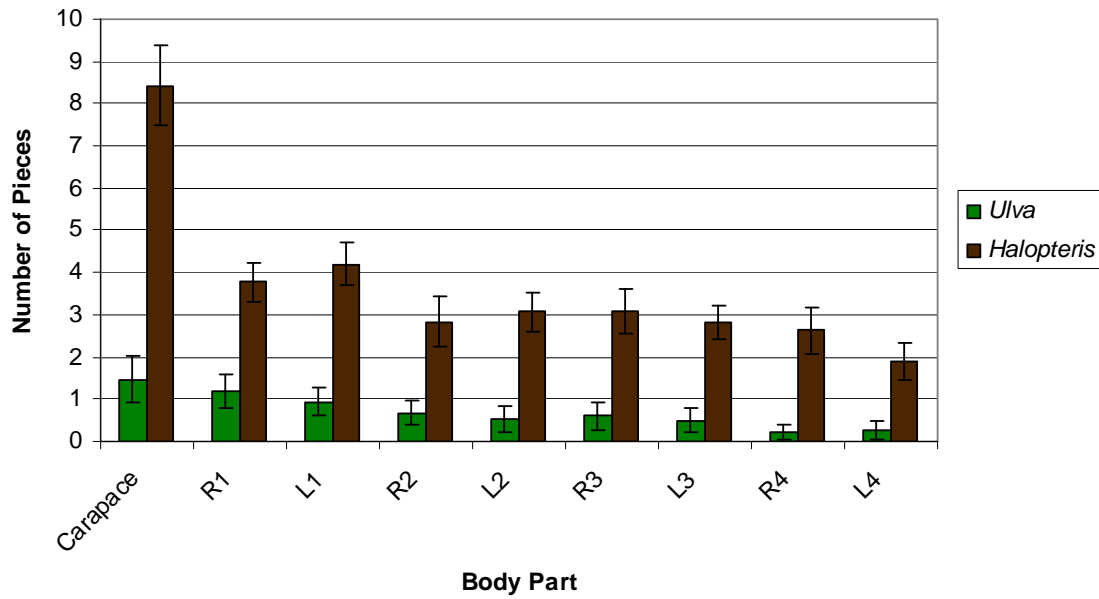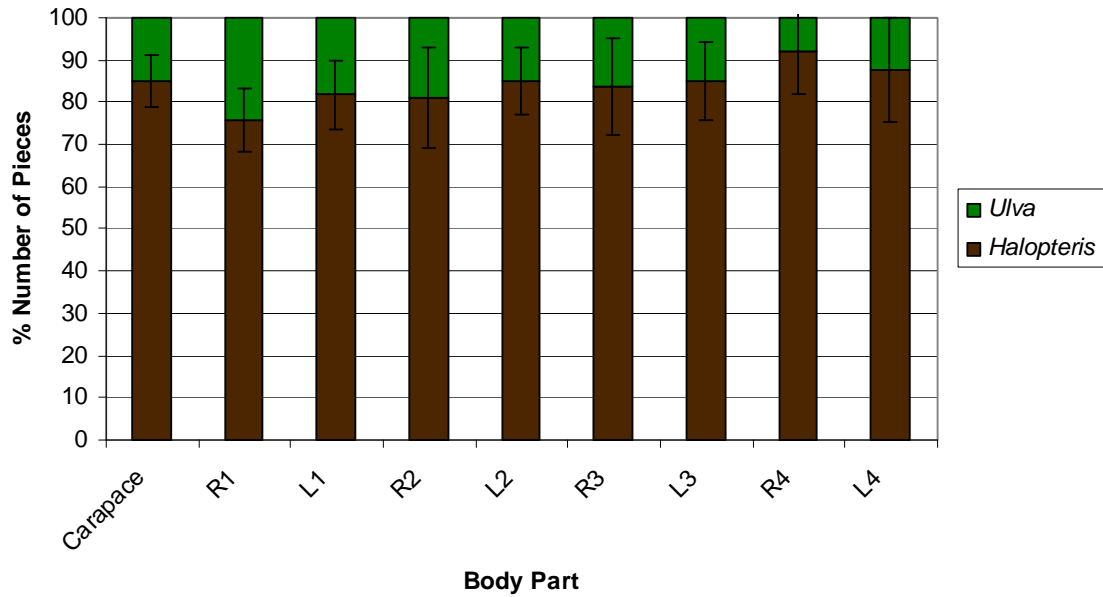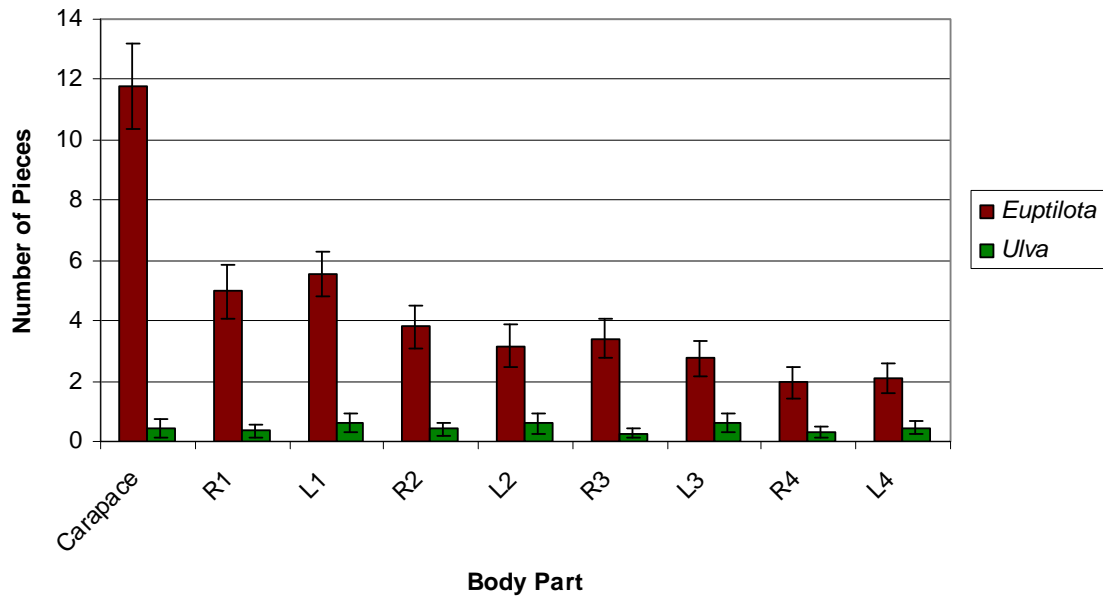*Halopteris* vs. *Ulva* (1:3 Ratio) Choice Experiment (n = 30)
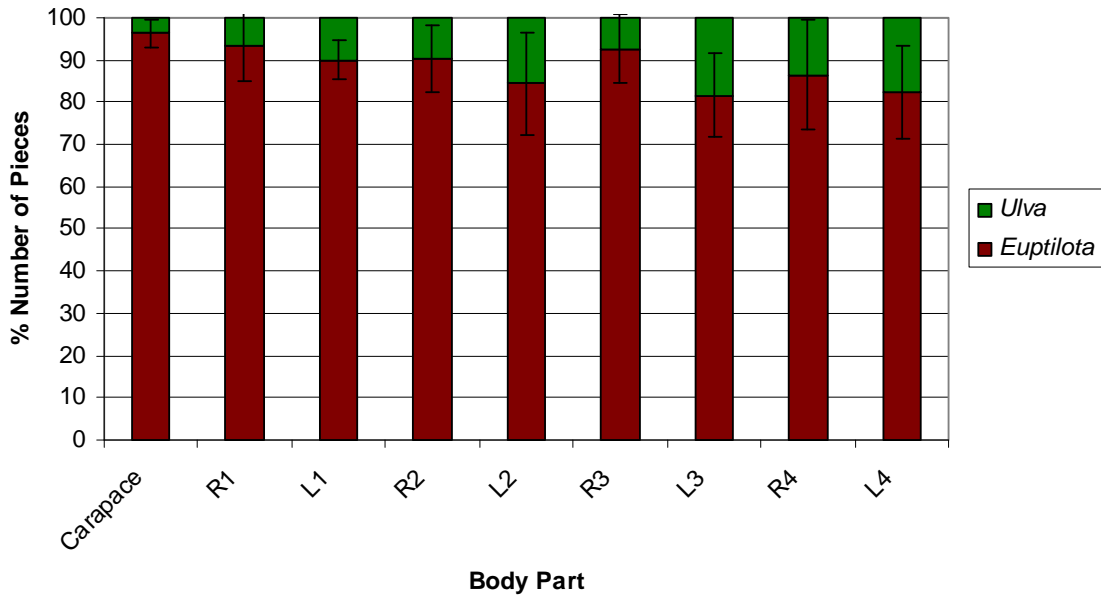
Figure 3.18 - Average Number of Pieces per Body Part
Euptilota vs. *Ulva* (1:1 Ratio) Choice Experiment (n = 29)

Figure 3.19 - Percentage Number of Pieces by Body Part
***Euptilota* vs. *Ulva* (1:1 Ratio) Choice Experiment (n = 29)**

Figure 3.20 - Average Number of Pieces per Body Part
***Euptilota* vs. *Ulva* (1:3 Ratio) Choice Experiment (n = 30)**
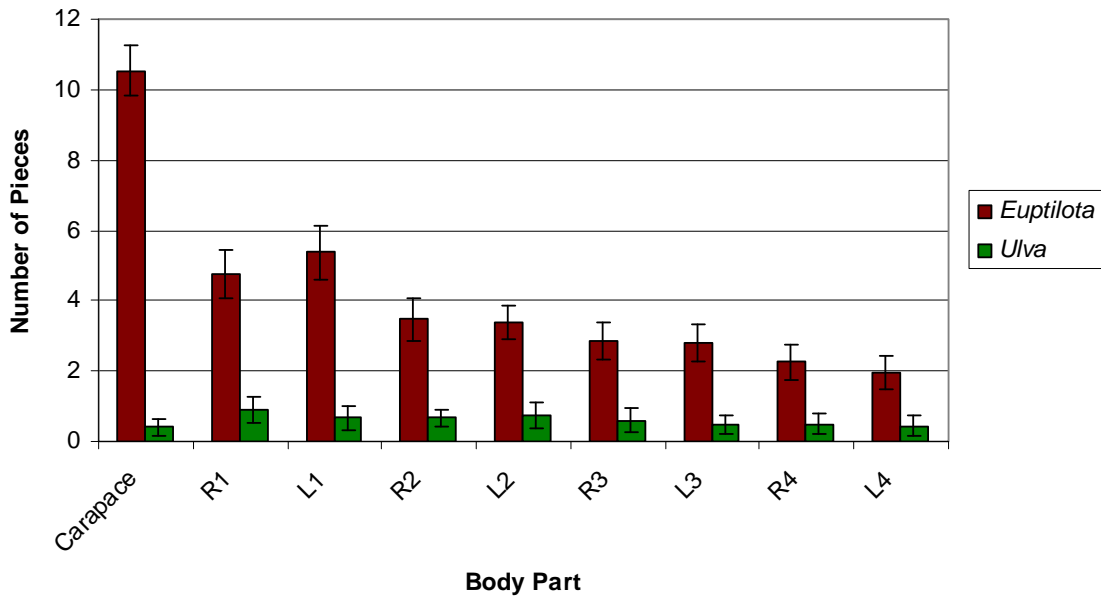
Figure 3.21 - Percentage Number of Pieces by Body Part
Euptilota vs. *Ulva* (1:3 Ratio) Choice Experiment (n = 30)

Figure 3.22 - Average Number of Pieces per Body Part
Euptilota vs. *Plocamium* (1:1 Ratio) Choice Experiment (n = 30)

Figure 3.23 - Percentage Number of Pieces by Body Part
Euptilota vs. *Plocamium* (1:1 Ratio) Choice Experiment (n = 30)

Figure 3.24 - Average Number of Pieces per Body Part
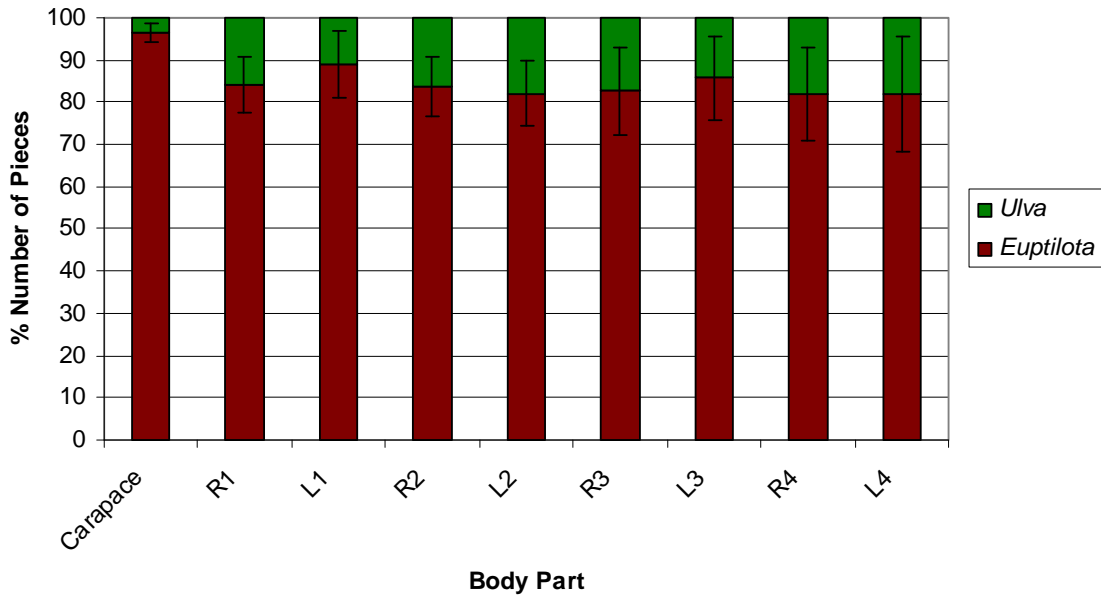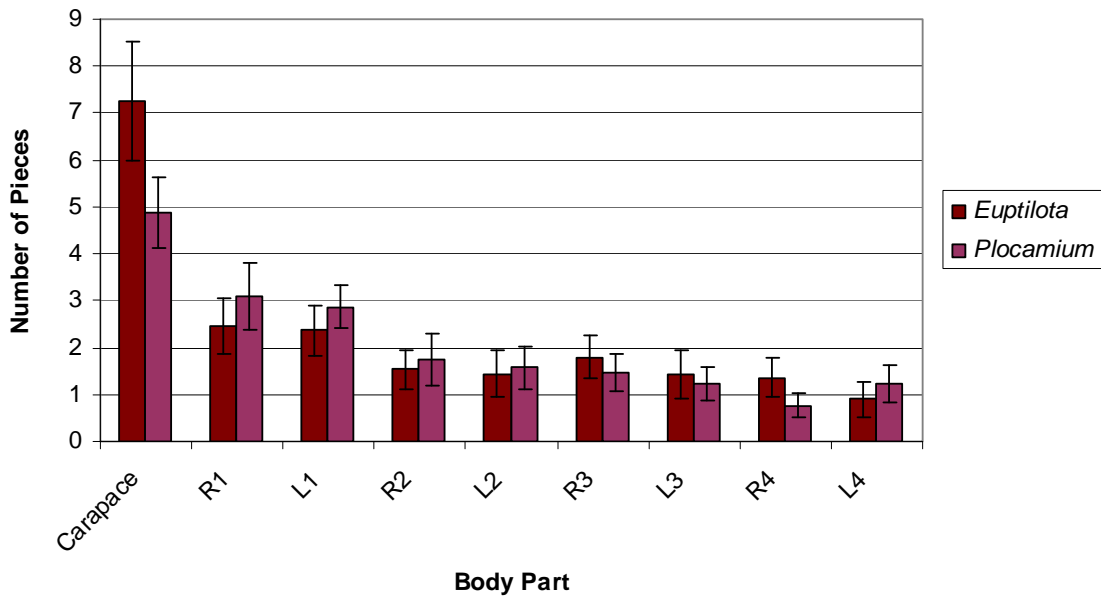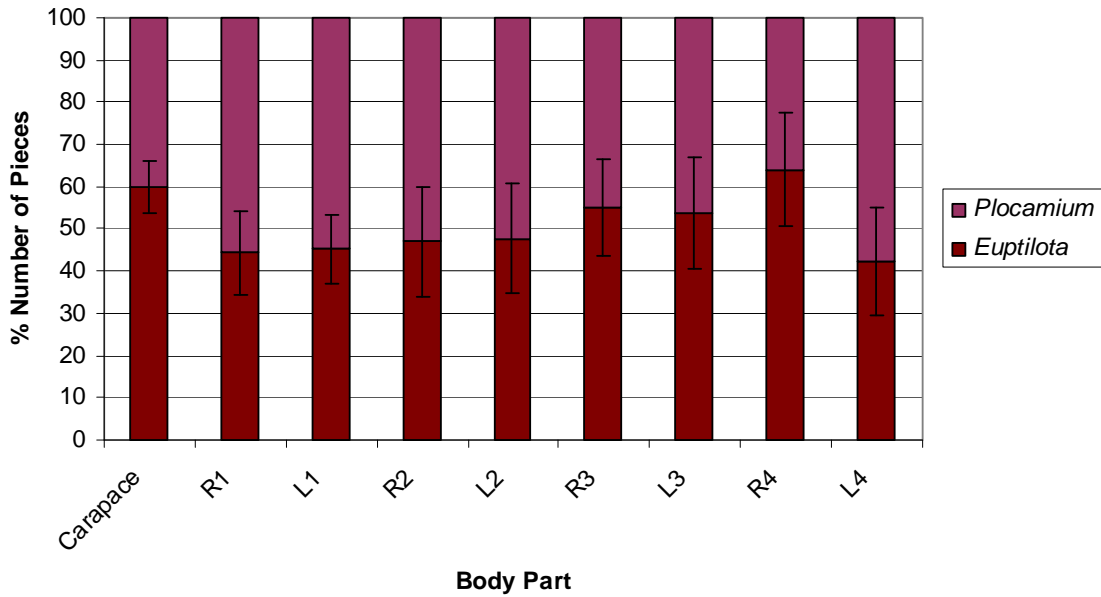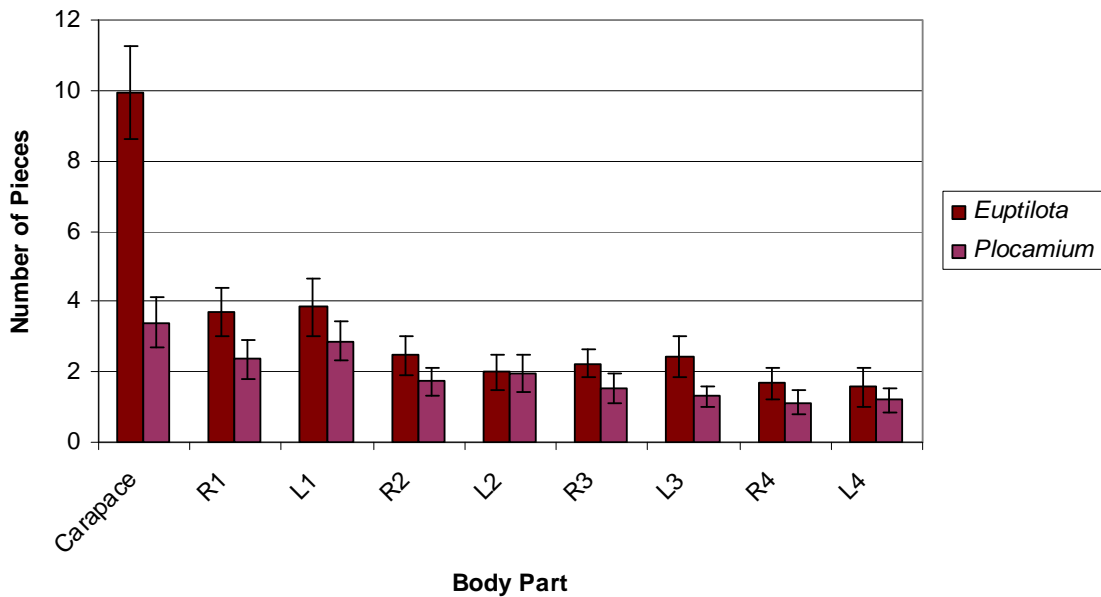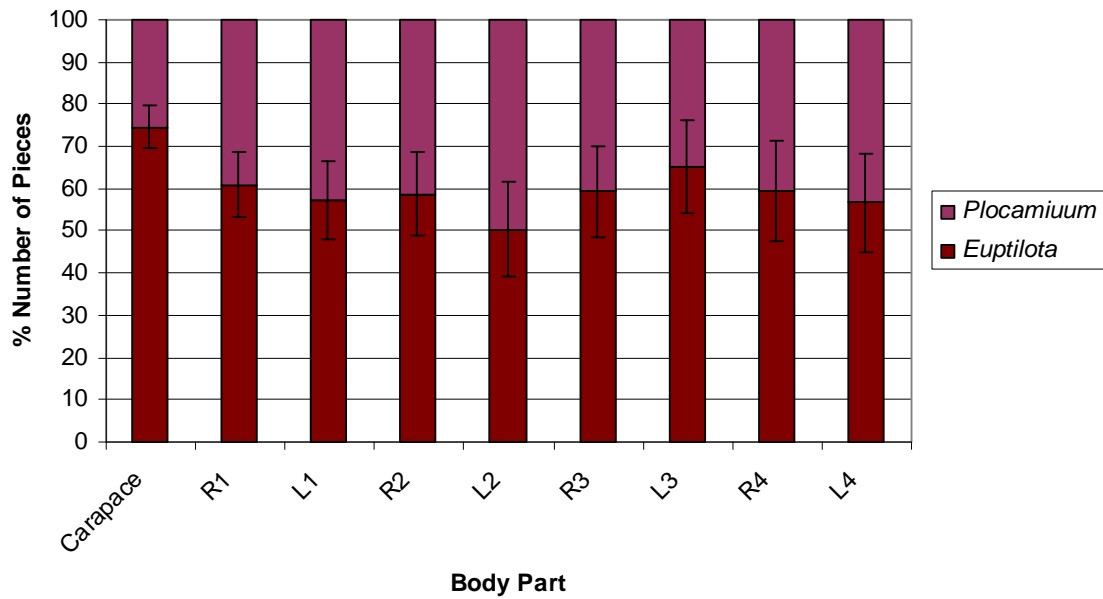*Euptilota* vs. *Plocamium* (3:1 Ratio) Choice Experiment (n = 30)

Figure 3.25 - Percentage Number of Pieces by Body Part
Euptilota vs. *Plocamium* (3:1 Ratio) Choice Experiment (n = 30)

Chapter 4: Background Change Experiments

Introduction

Camouflage is considered to be the biggest advantage of masking behaviour. In order for camouflage to be an effective strategy, the animal must maintain an appropriate match to its background. This is achieved in masking crabs by attaching pieces of algae and other sessile organisms found in their environment to their bodies. This causes the crabs to blend into their environment by changing their colour and hiding their outline and makes them look "less like crabs". This gives the crab some protection against visual predators.

Getty and Hazlett (1978) tested the camouflage theory by examining the spider crab *Microphrys bicornutus* to see if individuals that were displaced from a matching background exhibited a tendency to move to the appropriate background when given a choice. They also tested to see if individuals forced to be mismatched would increase their redecorating behavior to match the new surroundings. Both the habitat choice experiments and redecorating experiments failed to show any tendency for these individuals to actively redecorate to match their background. A mark-recapture study done on this species show that they have relatively low mobility. Getty and Hazlett (1978) thus hypothesized that this, together with the high turnover rate of the mask may be sufficient to maintain camouflage.

The purpose of this study was to examine what effect suddenly changing the background environment would have on *N. ursus* masking behavior. By allowing them

to dress up in one type of algae and then transferring them to a tank containing a different type of algae, they were forced to be mismatched. If the purpose of the masking behavior was only for camouflage, we would expect the crab to try to match its background as closely as possible and actively replace the mismatching pieces with new pieces from its new environment.

Methods

Thirty *N. ursus*, both male and female, were used in each background change experiment with carapace widths approximately 20 mm- 35 mm. *Euptilota* and *Halopteris* preference was further studied by allowing the crab to dress up in one type of alga, then examining the effect it would have if the background was suddenly switched to the other type.

The experimental setup was similar to that of the preference experiments. First the crabs were given only one type of alga, present in clumps attached to rocks in each corner of the tank. The crabs were then allowed enough time to fully dress, then switched to tanks containing only the other species of alga. The crabs were then left for 4 days (the approximate time to fully dress determined in the preference experiments), after which the mask was removed and measured to determine the amount of turnover that occurred as a result of the changing background.

The data were analyzed both by number of pieces of algae and total length. Also, the amount of turnover on each body part was examined. The amount of each type of algae was also compared to size of the crab, to determine if the size of the crab had an effect on the behaviour.

Results

Euptilota → *Halopteris* Background Change Experiment

When crabs completely covered in *Euptilota* were introduced to tanks containing only *Halopteris*, after four days on average about 36.65% of the mask was converted into *Halopteris*.

There was a significant difference in the turnover percentage based on the body part. The amount of turnover was least on the carapace and differed significantly from the last two pairs of legs. The amount of turnover on the first pair of legs was also significantly different from that of the last pair of legs (ANOVA f = 6.741, p < 0.0001; Figure 4.1). The number of pieces of *Euptilota* replaced with *Halopteris* was spread evenly across the body of the crab. There was no significant difference in the number of pieces turned over based on body part (ANOVA f = 1.60, p = 0.126; Figure 4.4).

There was a significant correlation between the percentage turnover and crab size. The percentage of *Halopteris* found in the mask after 4 days decreased significantly with increasing crab size (r^2 = 0.290; Figure 4.2).

Halopteris → *Euptilota* Background Change Experiment

When the crabs were first allowed to completely dress up in *Halopteris* and then switched to a tank containing only *Euptilota*, after four days they converted 29.93% of their *Halopteris* pieces into *Euptilota*.

There was a significant difference in the percentage turnover on different parts of the body. The amount of turnover was greatest on the carapace and was significantly different from the amount of turnover on the last 3 pairs of legs (ANOVA f = 5.50, p < 0.0001; Figure 4.3). There was also a significant difference in the number of pieces replaced with *Euptilota* based on location. The number of pieces replaced with *Euptilota* was largest on the carapace and significantly greater than on any of the legs (ANOVA f = 20.69, p < 0.0001; Figure 4.5).

There was no significant correlation between the percentage of pieces replaced with carapace width ($r^2 = 0.094$).

Discussion

If masking makes *N. ursus* cryptic, then a change in background would be expected to result in the total change of the mask so that the crab matched its background. When *Notomithrax ursus* was allowed to dress up completely in *Euptilota* and then placed in a tank containing *Halopteris*, after 4 days, ~36% of the mask was converted to the new background algae. Likewise, when the reverse experiment was done, allowing them to first dress up in *Halopteris* and then changing the background to *Euptilota* ~30% of the mask was converted to the new background material. This shows that there is some dependence on the background when choosing masking material, since in the preference experiments and natural mask composition, there was an overall preference for *Euptilota* shown. If they had a bias towards using *Euptilota* regardless of what their background was, you would expect less turnover in the *Euptilota* → *Halopteris*

experiment than in the *Halopteris* → *Euptilota* experiment, which is the opposite of what is seen.
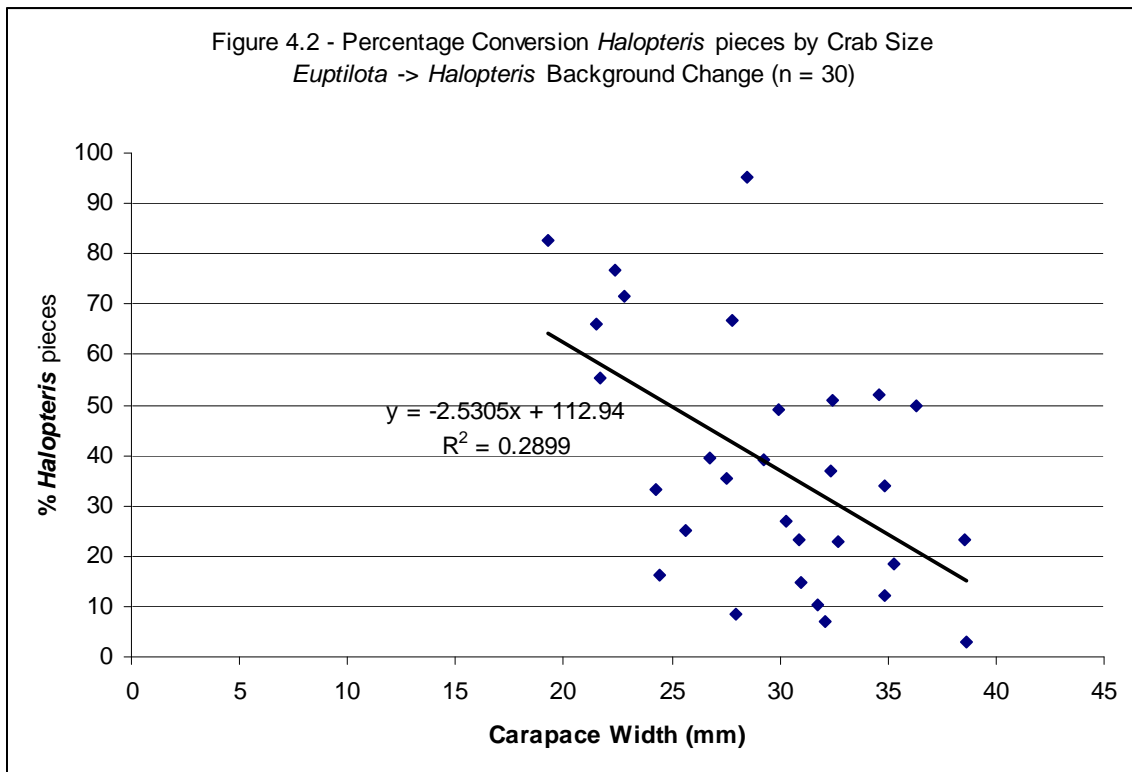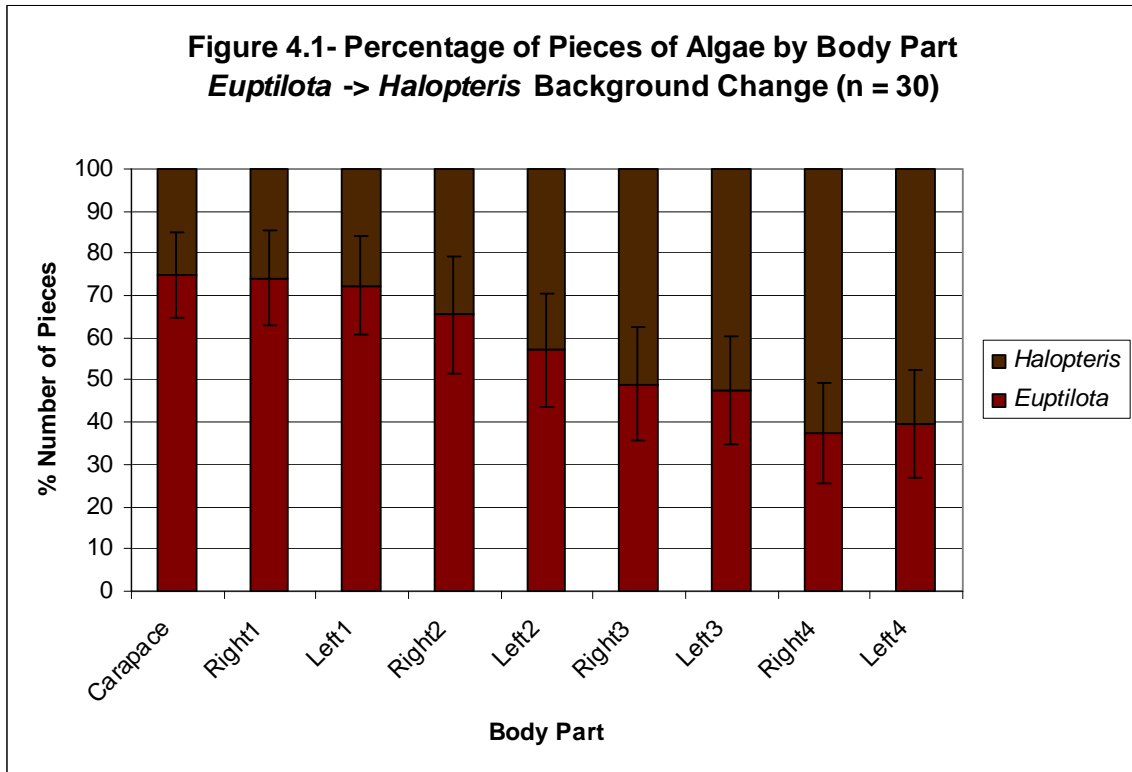
A preference for each algae being used selectively on different body parts is something else that must be considered. In the natural mask composition and preference experiments, the crabs displayed a strong preference for using *Euptilota* on the carapace, front legs and decreasing posteriorly. This is also seen in these experiments.

It would be expected that when replacing the mask, the crabs would operate in one of two ways: 1) by going "front to back" like their behavior dictates when dressing up from nudity or 2) by randomly replacing algae on any body part dependent on the proportion of algae normally found there – Carapace, first legs, second legs and so on.

In the *Euptilota* → *Halopteris* experiment, you can see evidence that the crab will randomly replace pieces evenly across its entire body, as there was no significant difference in the number of pieces of *Halopteris* by body part. This also closely resembles the normal distribution of *Halopteris* in the natural mask.

In the *Halopteris* → *Euptilota* experiment, the rate of turnover does not seem to be so random on different areas. The percentage and number of pieces of *Euptilota* that was added to the mask is greatest on the carapace, but otherwise evenly spread among the legs. This result could be evidence that the crab preferentially displaces pieces of algae proportionally to the total pieces present on that segment, or that the crab actively replaces more *Euptilota* on the carapace, because it actually has a preference for that species in that location. This second explanation is consistent with the results of the preference experiments and survey of natural mask data.

Graphs and Tables

Figure 4.1- Percentage of Pieces of Algae by Body Part
Euptilota -> Halopteris Background Change (n = 30)

Figure 4.2 - Percentage Conversion *Halopteris* pieces by Crab Size
Euptilota -> *Halopteris* Background Change (n = 30)

$$y = -2.5305x + 112.94$$
$$R^2 = 0.2899$$

Figure 4.3 - Percentage of Pieces by Body Part
Halopteris -> *Euptilota* Background Change (n = 28)
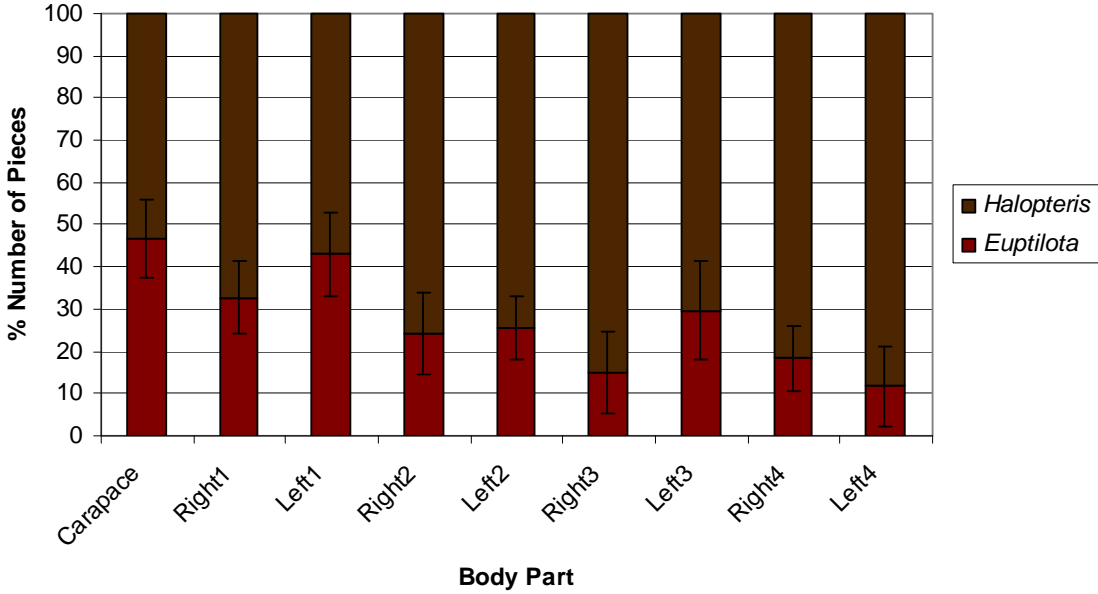
Figure 4.4 - Average Number of Pieces per Body Part
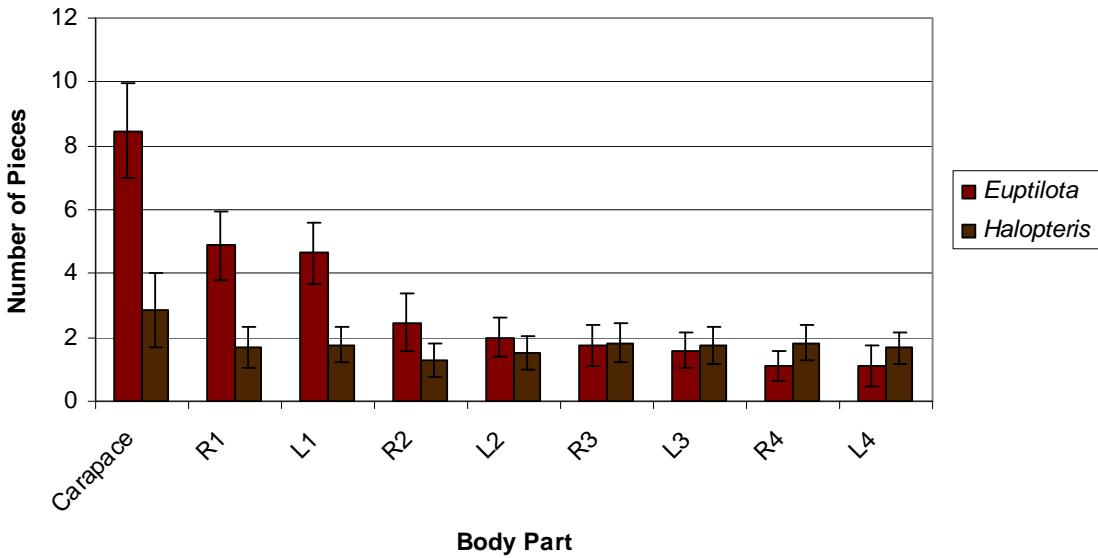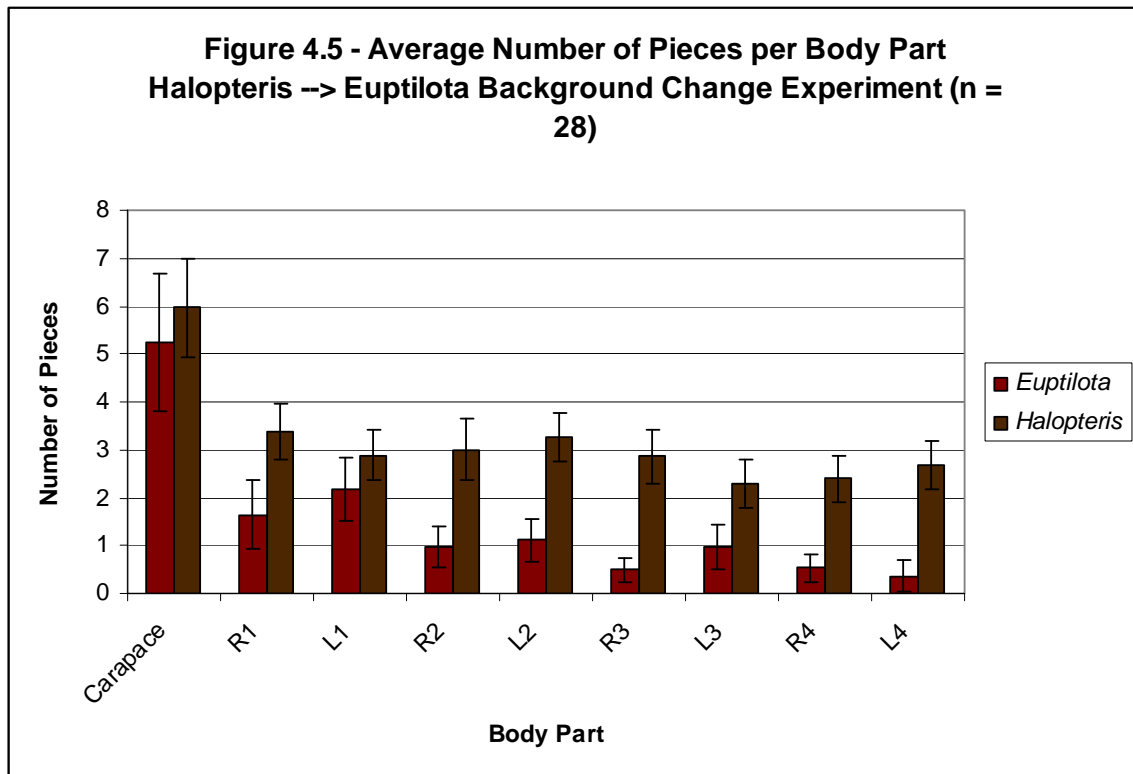*Euptilota* -> *Halopteris* Background Change Experiment (n = 30)

Figure 4.5 - Average Number of Pieces per Body Part Halopteris --> Euptilota Background Change Experiment (n = 28)

Chapter 5: Discussion and Conclusions

In this project, the algal preference of the masking crab, *Notomithrax ursus* was studied. The natural mask composition was examined and experiments were performed to determine the preference the crab has for certain types of algae and why.

In *Notomithrax ursus*, the mask can be assumed to serve the primary purpose of camouflage. Since the algae is thickly located across the entire body of the crab, it does a great job of obscuring the crab's outline. However, secondary purposes of the mask may still exist, especially since the composition of the algae is not consistent with what is found in the background. The crab may be able to successfully camouflage itself while still being selective about which algae it uses for other reasons.

N. ursus was seen to prefer three species of algae over others, *Plocamium microcladioides*, *Euptilota formosissima* and *Halopteris virgata*. *Plocamium* and *Euptilota* are red, branched algae and *Halopteris* is a brown foliose alga. Other species were also used in the mask such as *Corallina* sp, *Ulva* sp, *Dasychlonium* sp., among others. The most common species of algae that can be reasonably handled by the crabs found growing in their environment are *Halopteris* and *Ulva*. These species are usually very abundant near the Kaikoura seal colony where these crabs were collected. *Plocamium* and *Euptilota* do not grow in the intertidal where the crabs are found, but in deeper water. These species are broken and washed up to the shore where they are utilized by the crabs. Even though these species do not grow naturally near the collection site, pieces of each are usually pretty abundant along the shore, near and under rocks where the crabs hide.

Even though the three most used species in the mask are also among the most abundant in their habitat, the masking preferences of this crab cannot be explained by availability alone. As seen in the results of the experiments, the crabs usually preferred one algae species over the other when given two to choose from. This phenomenon is not consistent with the idea that the crabs randomly use whatever they happen to come across in the environment – to match the most abundant species in the background. The background does have some effect on the mask composition of the crab, but other hypotheses are necessary to explain why the crab often has a clear preference, even among the types it normally uses. Some of these possible explanations are handling time, morphology of the algae, seasonal variation, the use of the mask as food storage, and chemical defense.

Handling Time

Ideally the crab will use a species of algae that gives it the greatest amount of cover for the least effort involved in obtaining and using it. The rarity of *Ulva*, which is a very common species in the environment, in the mask may be explained by handling time. N. *ursus* uses this species very infrequently, however, another species in the same genus, *N. peronii*, which is found in the same areas as *N. ursus* does use *Ulva* frequently in the mask. This, and the fact that *Ulva* is sometimes found in the mask of *N. ursus* shows that the crab is able to handle the algae. However, differences in the attachment behaviour between the two species of crab may explain the differences in their preference. In *N. ursus,* there is a difference in the way algae is attached to the setae

depending on whether it is branched or thallose. Branched algae are inserted between and held by the hooked setae. Thallose algae, such as *Ulva* sp. may be inserted between the setae or impaled on them. (Woods and McLay, 1994a). Even though capable of using *Ulva* in a pinch, it may not be as easy to use as the branched types.

As seen in the preference experiments, there was evidence that the amount of *Ulva* usage in the mask increases with the size of the crab. This may be because the chelipeds are stronger and better equipped to cut and manipulate the algae when the crab is larger. This tends to suggest that handling time may be a factor.

Most of the types of algae found in the mask of N. *ursus* were branching species. They also were typically quite delicate species. There was an abundance of algae species in the environment that wouldn't be suitable to use because it is too large to be cut or manipulated by the crab. The age of the algae may also affect preference. Crabs may be able to mask with young algae, since it will commonly be smaller and softer, but as the algae grows it may begin to exceed the manipulative capabilities of the crab (Woods and McLay, 1994a).

In addition to the fact that certain species of algae are harder to handle, other aspects of algal morphology may be having an effect on their use as decoration. *N. ursus* shows a preference for branched algae instead of thallose algae. They especially seem to prefer the branching reds, *Plocamium* and *Euptilota*, which have a distinctive "fan" like structure. *Halopteris* is a more foliose species, which instead of branching out wider frequently like the reds, often just has longer pieces of the same width. This difference in structure may account for the preferential use of *Euptilota* and *Plocamium* in the mask. These red species, because of their "fan" structure are able to provide more cover than the

same length of piece of *Halopteris*. This may be why these two species are used preferentially on the carapace and front legs, where the outline of the crab needs more obscuring, especially to hide the eyes and chelipeds. The use of these branched species may also completely hide the movement underneath, allowing the crab to move its chelipeds to eat normally without giving itself away to predators. This may also explain the lack of *Ulva* in the mask. *Ulva*, being a thallose alga, doesn't broaden with the length of piece. In general, the pieces of *Ulva* that the crab did use were also very short, which wouldn't do very well to obscure the outline of the crab.

The structure of the algae may affect its potential use as crab size increases as well. *Halopteris* is more fragile than *Euptilota* and *Plocamium*. It falls apart relatively easily. This may account for the fact that the amount of *Halopteris* in the mask generally decreases as crab size increases. The crab may preferentially use *Euptilota* and *Plocamium* as it grows because these species are easier to cut in larger pieces and get the same amount of cover.

Also, it has been suggested that water turbidity may have an effect. In turbulent water, pieces of branched algae may be easier for the crabs to use since turbulent waters have less effect on branched algae (Mastro, 1981). The collection site at Kaikoura is quite turbulent, which may also explain the use of branched algae in the mask. It has also been suggested that the use of masking material may stabilize the crab in the event of a free fall (Sallam et al, 2007). However, if using a lot of thallose algae in turbid water, it may have the opposite effect.

The density and water absorption of the algae may also affect preference. *Halopteris* is a denser species than either *Plocamium* or *Euptilota*. This may explain why

the latter are found in much greater abundance on the carapace. Because of the positioning of some of the algae on the rostrum to be forward facing and "hang over" the front of the crab, heavier species may weigh the crab down or impede vision or movement. The branching lighter algae may be preferentially used also because they give a "drifting" movement when the crab is immersed, which may allow the crab to walk while still being unrecognizable as more than a clump of algae. Also, the lack of *Ulva* in the mask and the lack of *Halopteris* on the carapace may be explained by the fact that both of these species are very water absorbent compared to the branching reds. This obviously would have little effect on the crabs while immersed, but if the crab is ever exposed to open air, the extra water weight may impede movement, weigh down the algae over the rostrum, which may restrict the crabs feeding behaviour and its vision.

Seasonal Variation

Another factor which may affect the masking preferences of the algae is the seasonal variation in available species. From personal observations at the collection site, the three species used most commonly by the crab do not seem to vary in abundance depending on the time of year. *Halopteris* was found growing and *Plocamium* and *Euptilota* were found washed up on the shore all year long. *Ulva*, on the other hand did seem to vary seasonally. The abundance of *Ulva* was greater during the summer months than in the winter. This could be a possible explanation for why *Ulva* is not a preferred species. A preference for algae that would keep the crab camouflaged year round would be easier to evolve than a seasonal variation in preference. The crab may forgo using

Ulva because it will not be abundant year round, or may inhibit the crab from blending in during the months of its absence.

Food Storage

Food storage may also be a secondary function of the mask in this species. In a previous study, it was found that the masking preferences were correlated to the ingestion preferences in *N. ursus* (Woods and Mclay, 1994a). Also, separately examining the ingestion preferences, it was discovered that the crabs removed and ate certain species of their mask more than others. The most preferred types of algae were, in order, *Halopteris*, *Corallina*, *Plocamium*, and *Ulva* (Woods and Mclay 1994b). *Euptilota* was eaten very infrequently by comparison and was one of the least preferred food sources. These results are mostly inconsistent with my findings that the crab prefers to mask with *Euptilota*, *Plocamium* and *Halopteris*, in that order. However, the crabs in this study were collected from a different site, so there may be some geographical variation in the abundance of algae, or the masking preference of the crab.

Also, it would be expected that the preferred food items be stored in an easy to reach location on the crab's body – like the carapace, rostrum or first pair of legs. Woods and McLay (1994b) found that ingestion of mask material mainly involved removal from the carapace. The crab may also remove mask material from the carapace first, since while moving the legs would be visible and thus may be most important to keep covered (Woods and McLay 1994b). *Halopteris* is evenly distributed across the body, not preferentially placed on the carapace which contradicts its possible function as a

preferred food item. Although accessible on the rest of the body, we would expect that if the mask is serving a purpose for food storage, the preferred food items should be preferentially placed on the carapace, since ingestion of the mask mainly involves removal from this area (Woods and McLay 1994b). However, *Plocamium* is preferentially placed on the front of the crab, so food preference may account for this behaviour. Also, there was a clear preference for *Plocamium* displayed in the choice experiments. *Plocamium* is by far less abundant in the habitat than *Euptilota*, but it still has a significant preference for the mask. This may be a preferred food item, but its limited availability may make it appear to be less preferred as masking material in the natural mask. However, in the choice experiments, there was a clear preference for *Plocamium* over both *Halopteris* and *Euptilota*. This result may be consistent with the use of *Plocamium* as a food item.

The use of a preferred food item in the mask may be doubly beneficial to the crab because it would still provide camouflage while also giving the crab a backup source of food, if the crab is unable to find its preferred food items elsewhere. It was found that in N. *ursus*, the crab ingested significantly more of its mask when not given mussels as an alternative source of food (Woods and McLay 1994b).

There is also evidence of the mask being used for food storage in other species of crab. Kilar and Lou (1986) carried out an experiment on the dietary and camouflage preferences of the decorator crab *Microphrys bicornutus* on a Caribbean fringing reef. The predominant algae on the reef, *Laurencia papillosa* and *Acanthophora spicifera*, are also the crab's principal food and decoration resources, as indicated by stomach contents. They discovered that when the standing crop of the algae was high, the proportion of

these algae in the diet and on the carapace did not differ. However, when the standing crop was low, there was a preference for *L. papillosa* in both the mask and stomach contents. Their experiments showed that this crab prefers to not eat its camouflage when other foods are available, but when standing crop is low, it will readily consume its mask. The carapace flora serves as an alternative food reserve in this species.

A similar experiment done on the masking crab *Pugettia producta* showed that the crab eats the algae off of its own rostrum when it is isolated from food (Mastro, 1981). However, unlike *N. ursus*, this crab decorates only on its rostrum, which shows that food storage is most likely to be the primary purpose of the mask since this sparse covering is unlikely to camouflage it adequately.

Chemical Defense

Although there is no evidence for this type of behaviour in *N. ursus*, in other species of masking crab, the mask can serve a secondary purpose of a chemical defense system for the animal. The use of such algae may deter omnivorous predators from accidentally ingesting the crab because the alga is known to be noxious to them, or may cause carnivorous predators which discovered the crab to spit it out once they get a mouthful of the unpalatable algae.

Although it is not known which species of algae in New Zealand are noxious to fish and other predators, there are some other species of *Plocamium* in other parts of the world which are known to be toxic, including *Plocamium hamatum* collected in Queensland, Australia (de Nys et al. 1991) and *P. cartilagineum* collected in Chile

(Argandona et al. 2000). It is therefore, possible that the New Zealand species of *Plocamium*, including the one used as masking material could be noxious as well.

There is evidence for chemical defense in other species of masking crab. For example, Stachowicz and Hay (1999) showed that the decorator crab *Libinia dubia* selectively decorated with the chemically defended brown algae *Dictyota menstrualis*, but treat this plant as a low preference food. Common omnivorous fishes that are potential predators avoid eating *Dictyota* because of its potent chemical defenses. The crabs in the field experienced significantly less predation than crabs decorated with an alga that is not chemically noxious to local fishes. They also showed that the *Dictyota* metabolite (dictyol E) that most strongly deters feeding by fish is the metabolite that determines masking choice by this crab.

Conclusion

In conclusion, although the mask is primarily used for camouflage, the preference in masking materials cannot be entirely explained by *N. ursus* trying to perfectly match its background. The crab manages to maintain a suitable level of camouflage even when preferentially choosing some species of algae over others. There are a variety of factors that may contribute to this preference including the handling time of the algae, seasonal variation in algae abundance or the secondary purpose of the mask as a food store or chemical defense system. These factors are not mutually exclusive and may all significantly contribute to the preferences seen in this species.

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