

# **Interaction strength in an intertidal rocky habitat: an observational approach**



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## Abstract

Knowing the structure of the food web within a community is of specific importance for the understanding of the dynamics of a community, which can lead to better predictions on how the system will react on (environmental) changes. For each combination of two species related to each other as predator and prey, the total impact of the predator species on the prey species can be calculated. This 'species impact' can be quantified by multiplying the effect individual predators have on the (entire) prey population – i.e. the 'per capita interaction strength' – with the density of the predator population. The most common approach of studying interaction strength between species in a community has been an experimental one. Recently, an observational approach has been developed, as an experimental approach can not be applied for all predator-prey relations. The observational approach has originally been developed to study interaction strengths between shorebirds and their prey. In this study the feasibility of the observational approach to study the effect of a marine predator - the starfish *Pisaster ochraceus* - has on various prey species of an intertidal rocky shore community is tested. Results show that *Pisaster* feeds selectively upon mussels even though other prey species are available. Acorn barnacles are avoided when possible or eaten in relation to their abundance. At the two sites tested *Pisaster* has a stronger per capita effect upon the mussel population than on the acorn barnacle population; other prey species remained more or less unaffected by the predation activity of the starfish. The predator has a stronger per capita effect upon the mussel population than on the barnacle population. In comparison with a previous study on the same species, the 'per capita effect' and 'species impact' were surprisingly low. Even though the starfish has proven to be a 'keystone species', the effect of the starfish on the prey population found in this study was only comparable with that of a weak predator. The feasibility of the observational approach is discussed and it is indicated for which parameters more experiments are required before the observational approach can be used for this starfish.

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## Introduction

The study of community dynamics and the processes underlying it is an important one. It may lead to a better understanding of the often complex community dynamics in itself (Laska and Wootton 1998; Wootton 1997; Paine 1992; Navarrete and Menge 1996), but it may also lead to a better insight on how community dynamics can be useful to nature conservation ends (Navarrete and Menge 1996; Paine 1992). This may increase the ability to predict the influence of environmental changes (either caused by natural events or human impact) on a community (Menge *et al.* 1997; Wootton 1997).

Knowledge on the relations between species within a community is of specific importance for the understanding of the dynamics of a community. A way of studying relations between species is through food webs. Food web structures can be determined by the presence or absence of linkages between organisms of different trophic levels (Elton 1927). In this way the relations between species are identified, but no quantified measure of the strengths of these relations is given (Paine 1980). In order to quantify a relation between two species that relate to each other as predator and prey, two measures can be used; 'electivity' and 'interaction strength'. Electivity is a relative measure derived from the predator's feeding behavior. It quantifies whether a predator prefers or avoids a certain prey species. If a prey is abundant in the diet relatively more than available in the field, the prey is preferred. Interaction strength, on the contrary, is an absolute measure. The effect of one individual predator on a population of a certain prey species is called the 'per capita interaction strength'; the effect of the total predator population 'species impact' (Wootton 1997). Species impact can be calculated by multiplying the per capita interaction strength with the density of the predators. Species impact can thus be large for two reasons: 1) the density of the predator in the system is high and 2) the per capita interaction strength of the predator is high. Species that have a large influence on a certain prey are called 'strong interactors'. When the influence is out of proportion large relative to the abundance of the predator species, strong interactors are called 'keystone species'. Both strong interactors and keystone species have a clear effect on other species. Removal of these species may have major consequences for the community, while removal of 'weak interactors' hardly changes the system (Paine 1992; Navarrete and Menge 1996). Within a community only a few species within a system are strong interactors and even less are keystone species. Most of the species appear to have hardly any effect on other species in the community.

Whereas electivity can be studied by observing predator diet and prey abundance, interaction strength is most often studied experimentally (e.g. Sanford 1999; Menge *et al.* 1996; Navarrete and Menge 1996; Paine 1992). Differences in community structure in situations with and without predator species (i.e. enclosure and exclosure treatment) are considered to be a measure of per capita interaction strength or species impact. Clearly not every system and every organism within a system can be easily manipulated experimentally (Wootton 1997). The larger and the more mobile the organisms or systems are, the less attractive and feasible the experimental approach will be. Being aware of this Wootton (1997) developed an approach to measure interaction strength (both per capita interaction strength and species impact) observationally, using shorebirds in rocky shore communities on the Pacific NW Coast.

The new observational approach is not yet tested on its applicability in other communities. In this study the applicability of the new observational approach is studied in a marine predator-prey community: the starfish *Pisaster ochraceus*

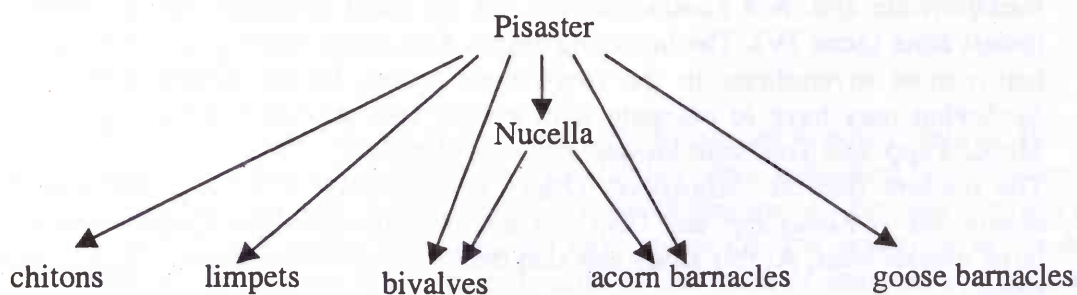
(hereafter referred to as *Pisaster*) and its prey species. This community is well studied experimentally (e.g. Sanford 1999; Menge *et al.* 1996; Navarrete and Menge 1996; Paine 1992). The results of the experimental approach are compared with results of the observational approach of this study.

# Methods

## Study species

Pisaster is a relatively large marine predator living on the rocky shores of the West Coast of North- America (from Alaska to Baja California (Ricketts and Calvin 1952). The ecological role of Pisaster is well studied; Pisaster appears to constitute a distinct subfood web of the intertidal community (Paine 1966). The starfish has almost no important predators of its own (see Picture 1) (Paine 1966). Only Glaucous-winged Gulls (*Larus glaucescens*) occasionally forage on Pisaster (Wootton 1997). The starfish can therefore be regarded as a top carnivore preying upon lower trophic levels (see Picture 1).

Results of experimental research have reported that Pisaster has a disproportional large effect upon the prey population relative to its abundance; the starfish is therefore known as a keystone species (Paine 1969). Pisaster seems to have a strong preference for the mussel *M. californianus* (Landenberger 1968; Paine 1969), the competitively most dominant species of the intertidal benthic community (Paine 1966, 1974; Harger 1972). The continuous and sharply defined edge of the lower limit of mussel beds of *M. californianus* is thought to be established by the predatory activity of the carnivore (Paine 1966; 1974). With its preference for the competitive dominant species, Pisaster enables the less dominant species to establish themselves in the environment (Paine 1974). Thereby species diversity increases, even if considers only those species directly attached to the rock surface. This restriction is necessary because a species-rich assemblage is associated with the mussel bed (> 300 species, Suchanek 1979)



Picture 1: Food web structure of Pisaster and its prey assemblage.

## Study sites

Four sites where Pisaster is known to occur, are chosen along the Strait of Juan de Fuca, Washington State. Three are located at the outer coast of the Olympic Peninsula, while the fourth study site is located in the protected waters of northern Puget Sound (see Picture 2a).

The western-most site (site 1), 'Tatoosh' Island, is located approximately 0.4 km of the northwestern tip off Cape Flattery (Wootton 1997). The island consists of many small islets, with rocky shores that are exposed to severe wave action during the whole year (Harley 1998; Paine 1974). Not all the rocky benches on 'Tatoosh' are similar in their habitats. To obtain a more representative view the rocky benches on 'Tatoosh' are subdivided into three study sites: 'North Island' (site 1a), 'Strawberry Draw' (site 1b) and 'Simon's landing' (site 1c) (Paine and Levin 1981) (see Picture



2b). 'North Island' and 'Simon's Landing' have quite similar habitats consisting of large rocky benches covered with mussel beds, whereas 'Strawberry Draw' consists partly of rocky benches and partly of a large boulder field.

The two study sites located on the mainland of the Olympic Peninsula are site 2 near Neah Bay, at the eastern side of Cape Flattery, and site 3 'Slip Point' at the eastern tip of Clallam Bay. The 'Neah Bay' site consists of two rocky benches that are separated by an extensive sand beach. Both benches are small northern facing rock habitats. The unpredictability of sand burial or sand scour is likely to have an influence on the community here (Menge *et al.* 1994). Site 3, 'Slip Point' at 'Clallam Bay' is one continuous rocky shore with extensive rocky benches separated by boulder fields. Wave action on both sites is less severe than on Tatoosh.

The fourth and eastern-most study site, 'Saddlebag Island' is situated in protected waters of Padilla Bay. The island consists of a continuous rocky shore with parts of smaller rocks.

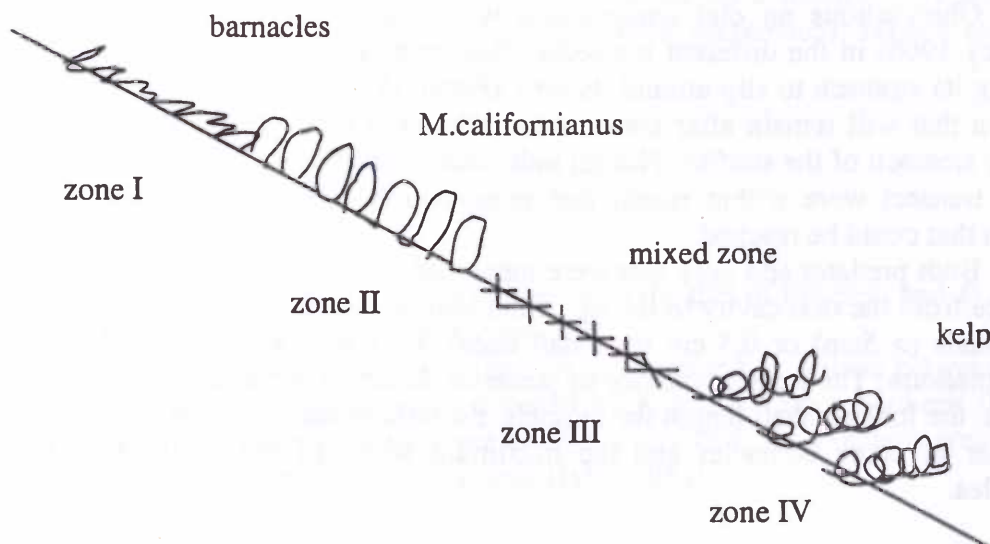
### Site characteristics

The rocky shores on 'Tatoosh' mainly consist of large rocky benches that exhibit a well-defined zone pattern, with roughly four clearly distinct zones (Picture 3) (Harley 1998; Paine 1974; Paine and Levin 1981). The upper zone (zone I) is mainly occupied by barnacles. Beds of large California mussels, *M. californianus*, dominate the next zone (zone II). A mosaic of disturbance patches characterizes the mussel beds. In these patches earlier succession stages occur with different species such as the blue mussel *Mytilus trossulus*, limpets, goose barnacles *Pollicipes polymerus* and predatory whelks *Nucella spp.* Below the mussel bed a mixed zone (zone III) occurs with species as limpets, goose barnacles, acorn barnacles *Chthamalus dalli* and some red algae. This zone provides cover for the juveniles of the species that live in zone II. Both coralline algae and brown algae species such as *Hedophyllum spp.* and *Laminaria spp.* are the most abundant species found in the lowest zone (zone IV). The browsing chiton *Katharina tunicata* is the most abundant herbivorous invertebrate in the two lowest zones. In the lowest zone the chiton *Katharina* may have to compete with several less abundant chiton species such as *Mopalia spp.* and *Tonicella lineata*, and some limpets.

The boulder field at 'Strawberry Draw' is characterized by rock surfaces that are dominated by *Fucus spp.* and *Ulva spp.* and patchily distributed large mussels, but no large mussel beds. At this study site also the large herbivorous snail *Tegula funebris* occurs.

The two mainland sites are more or less similar in composition to the sites on Tatoosh. The rocky benches at 'Saddlebag Island' exhibit, however, a distinct pattern from the other sites, due to the low wave action here. At this site the number of *Balanus glandula* are reduced. Hardly any mussel occurs on the island; the ones that do occur are small individuals of the early colonizing blue mussels *M. trossulus*. The lower zone is dominated by brown algae, mainly *Fucus spp.* (Harley 1998).





Picture 3: Four distinct zone pattern on rocky shores on 'Tatoosh' Island (per. obs. Paine)

### Sampling periods

Data was collected between June and September 1999. Samples were taken during spring tide periods when the minus tides made the rocky shores available. Spring tide periods were almost always twice a month. In total 'Tatoosh' was visited 5 times for periods of 3 to 4 consecutive days. 'Clallam Bay' was visited 8 times and 'Neah Bay' 6 times. 'Saddlebag Island' was visited once in early August for four consecutive days, and one more time in fall (end of November).

### Data collection

Within each site 'transects' were the unit of measure in which data on starfish density and consumption as well as prey availability were measured. The number of transects per study site varied from 3 to 8. A transect represented the area in which the starfish could forage during high tide, but only above the low waterline as the data were collected during low tide. At study sites where beds of mussels occurred, the lower border of beds of *M. californianus* was used as the upper limit of a transect. At 'Saddlebag Island' where mussel beds were absent, the upper limit was more arbitrarily determined. The homogenous characteristic of the benthic community along the shore determined the length of the transects. Thus not only the width of transects varied, but also the length (varying from 2 to 42 meter). Differences in transect surface was corrected for in the data analysis (see calculations in 'Food availability')

### Population structure of starfish

The number of *Pisaster* was counted per transect, permitting the density per square meter to be calculated. The average starfish density of all transects (weighted per transect area) within a study site was taken as average starfish density for that site. The density might be an overestimation for the total area of the study site, as sampling was likely to be biased by the transects where starfish occurred; data were not collected at transects where starfish did not occur.

## Diet composition

Observations on diet composition were made recording stomach contents (Mauzey 1966) in the different transects. *Pisaster* externally digests its prey (i.e. by everting its stomach to slip around its prey (Feder 1959). As all prey has an external skeleton that will remain after consumption, the prey items are easily visible in the cardiac stomach of the starfish. Not all individual starfish counted for population size in the transect were within reach; diet composition could only be obtained from starfish that could be reached.

Both predator and prey size were measured. Starfish size was measured as the distance from the oral cavity to the tip of the longest arm (to the nearest cm for large individuals ( $> 5\text{cm}$ ) or 0.5 cm for small ones). Prey size was measured as longest linear measure: The longest anterior to posterior distances were taken for limpets and chitons, the longest shell length for mussels, the columellar length of snails, the basal diameter of acorn barnacles and the maximum width of the shell base of goose barnacles.

## Food availability

In most transects three zones could be distinguished: 1) the lowest half meter of the mussel bed (zone II) was the upper zone, 2) the mixed zone the mid-zone and 3) the coralline - and brown algae zone the lower zone. To estimate food availability corrected for differences in zone characteristics, quadrates were taken in every zone. In most zones 10 quadrates were taken. Only in some cases sample size was smaller; this is corrected for. The small and more abundant acorn barnacles were counted within a  $5 \times 5\text{ cm}$  quadrat and the more mobile and rare species as the snail *Tegula* and the chitons (*Katharina tunicata*, *Tonicella lineata* and *Mopalia* spp. taken together) were counted in a block of  $20 \times 20\text{ cm}$  (see Table 1). All others were counted in a  $10 \times 10\text{ cm}$  quadrat.

To get an indication of what prey size was preferred by *Pisaster*, individuals of four prey species were divided into length categories; three categories for mussels *M. californianus* and chitons, and two for limpets and barnacles (see Table 1).

Table 1: Used measure of quadrat size and length categories for different prey species

species	quadrat size	length categories
Barnacle spp.	5*5	(s)<1 ; (l) >=1
<i>M. californianus</i>	10*10	(s) <1 ; (m) >=1, <3 ; (l) >=3
<i>M. trossulus</i>	10*10	-
Limpet spp.	10*10	(s)<1 ; (l) >=1
<i>Nucella</i> spp.	10*10	-
<i>P. polymerus</i>	10*10	-
Chiton spp.	20*20	(s) <1 ; (m) >=1, <3 ; (l) >=3
<i>Tegula funebris</i>	20*20	-

A slightly different method was used in sampling the boulder fields at 'Strawberry Draw'. Starfish in a boulder field were difficult to divide in sample transects as this habitat was more homogenous. Here the prey density within the near vicinity (1 m in all directions) was taken to estimate the prey availability for the starfish.

## Data analysis

### Food preference

The data on prey availability per square meter per study site ( $P_i$ ) together with the mean *Pisaster* diet composition per starfish per study site ( $r_i$ ) was used to

calculate the selective feeding behavior of *Pisaster* on a specific prey species in the presence of several other prey species (i.e. food preference); Ivlev's electivity ( $E$ ) formula was used (Ivlev 1961):

$$E = \frac{(r_i - p_i)}{(r_i + p_i)}$$

with  $r_i$  the relative content of a prey species in the diet of *Pisaster*, and  $p_i$  the relative value of the same species in the environment.

High preference for a prey species is expressed by values between +1 and 0. Avoidance of prey species is represented by negative values between 0 and -1. A value near 0 is taken as neither preferred nor avoided; the predator preys upon this species in proportion to their abundance (Ivlev 1961).

#### Food availability

The area of a zone within a transect and a transect within a study site could not be standardized to one size, therefore differences in size of areas and size of transect could occur. To correct for differences in area extent, the mean density for each prey species per transect was calculated as the number of individuals weighted by the proportion of the zone area. This was defined as the area of one zone divided by the sum of areas of all zones. The mean food availability for each study site was weighted by the proportion of the transect area. This was calculated as the ratio between the area of one transect divided by the summation of area of all transects.

In the boulder field the mean value of the data on all starfish was taken to calculate food availability and diet composition.

#### Interaction strength

Only for two study sites 'Saddlebag Island' (site 4) and 'North Island' (site 1a) on 'Tatoosh' the per capita interaction strength and species impact per prey species and length category was calculated.

$$pcSI = -\rho\phi(1/\delta)\lambda$$

This equation is derived from Wootton's equation (1997) used to calculate per capita interaction strength in a shorebird-rocky shore assemblage. The consumption rate of *Pisaster* ( $\rho$ ) is defined as the number of prey consumed per feeding starfish per time and  $\phi$  is the fraction of the population of the predators that were actually feeding. The number of prey that is available in the field ( $\delta$ ) is determined by the number of individuals of each prey species per square meter. The proportion of time the rocky shores (Wootton 1997) was accessible for the starfish ( $\lambda$ ) was assumed to be 1 as the digestion of prey continued during low tide (Paine 1969). Species impact could be calculated by multiplying per capita interaction strength by the predator density ( $\beta$ ).

No data could be found on *Pisaster*'s daily consumption rate ( $\rho$ ), neither in this study as in others. As field observations suggest that *Pisaster* feed twice a day corresponding with the two periods of immersion (Paine 1969), the number of prey individuals found in the diet per starfish per tide multiplied by two was assumed to be the daily consumption rate. The daily consumption rate ( $\rho$ ) of *Pisaster* on large mussels (length of 4 to 5 cm) reported by Sanford (1999) and Menge *et al.* (1996) was



used as the daily consumption rate of *Pisaster* on the largest length category. Sanford obtained feeding rates of *Pisaster* from lab experiments with the starfish. He found feeding rates of about 2 mussels a day (depending on water temperature); feeding rate of the starfish had a positive relation with water temperature. As water temperature changes during the year and depends on geographical location, the feeding behavior of *Pisaster* is likely to depend both on season and location. With increasing temperature in spring the feeding activity increases to be highest in the summer months from June until August. In September the activity drops again to be low in the winter months (Mauzey 1966, Paine 1969). Menge *et al.* (1996) estimated feeding rate of *Pisaster* in the field. They determined differences between mussels disappearing per day in areas with and without *Pisaster*. The estimated number of *Pisaster* per area was used to generate a per capita feeding rate. Daily consumption rate of *Pisaster* was found to be depending on wave exposure. At exposed rocky shores starfish consumed less prey items than when it would forage on a wave protected shore. In this study I used daily consumption rate on large mussels of 2 per day.

### Statistical analysis

Statistical tests were performed in JMP (version 3.2.6 for PW Macintosh, SAS Institute Inc.). 'One-way ANOVA' were used to test whether the mean ray lengths of *Pisaster* at the six study sites differed. Post hoc Student's t-tests were used for pairwise comparisons between sites.

The same tests were used to test differences between starfish densities between the study sites. No statistical analysis could be performed on data on electivity and per capita interaction strength as sample size was too small.

## Results

### Population structure

#### Predator density

The abundance of *Pisaster* could not be shown to vary significantly between five of the six study sites (see Figure 1a and Appendix 1a). Only at 'Simon's Landing' *Pisaster* did occur in a significantly higher density (One-factor ANOVA  $F_{v1,v2} = 3.96$ ,  $P < 0.009$ ). The mean density of starfish on this study site was more than two times the density that occurred at the other sites.

#### Predator size

*Pisaster* size varied from site to site (see Figure 1b and Appendix 1b). Starfishes at 'Saddlebag Island' were significantly smaller (mean size 11 cm) than the ones found at the other five study sites (mean size 16 cm) (One-way ANOVA  $F_{v1,v2} = 63.2551$ ,  $P < 0.0001$ ). The differences in mean size of the starfish population at these sites were small, but sometimes significant.

#### Feeding activity of predator

The feeding activity of *Pisaster* depended on site (Appendix 2). Starfish were found feeding about fifty percent of the time at study sites at Clallam Bay, Neah Bay, 'North Island' and the rocky bench of 'Strawberry Draw'. Fewer percentage of the starfish population was feeding in the boulder field of 'Strawberry Draw' and on Simon's landing. On 'Saddlebag Island' the feeding activity of starfish was fewest; only 29 % of the starfish were feeding.

#### Prey size

The starfish at the six study sites differed in their prey choices concerning length of prey individuals (see Figure 2). *Pisaster* at 'Saddlebag Island' and 'Neah Bay' had mainly small prey individuals (smaller than 1 cm) in their stomach, while the starfish of the other four sites consumed larger prey. Starfish at 'North Island' and 'Strawberry Draw' did not even consumed prey individuals smaller than 1 cm. The length of prey individuals occurring in the diet of starfish ranged mostly from 0.5 to 7 cm. However, *Pisaster* occasionally preyed upon prey individual with a length of 16 cm.

At 'Saddlebag Island' and 'Neah Bay' where starfish preyed mainly upon small prey individuals, the number of prey taken per meal was high. Sometimes more than 20 individuals could be observed in the starfish's stomach. At the other locations starfish took larger, but fewer prey at a time. At 'Simon's Landing' and 'Strawberry Draw' *Pisaster* did not take more than 5 individuals per meal.

### Interaction strength

#### Sample size

When no new species were observed in the diet of the predators, the curve of cumulative numbers of prey species in the diet of the predator would approach an asymptote. The slope of the curve therefore gave insight whether the sample size was large enough. If the slope was very small the chance of finding new species in the diet becomes low and sample size was likely to be sufficiently large. For most of the studies the sample size were sufficient (see Figure 3); however, the sample size at



'Simon's Landing' and 'Strawberry Draw' might have been too small. The results of the research on these two study sites might need to be interpreted cautiously.

### Prey species

#### *Food availability in field*

In general the composition of the prey community in the field did not vary much between the study sites (see Figure 4 and Appendix 3a). Barnacles were the most abundant prey at almost all sites with about 60 % of the total number of prey. Only on 'Saddlebag Island' the proportion of barnacles was much higher than that, the prey community consisted almost only of barnacles. At 'Simon's Landing' the relative abundance of barnacles was much lower with about 30 %.

The second most abundant prey species were mussels. The abundance of mussels differed per site, ranging from less than 5 to about 40 % in the diet. At most sites the mussel species occurring were California mussels. *M.trossulus* were rare at all sites except at Saddlebag Island. Here *M.trossulus* was the only mussel species occurring.

Compared with the abundance of barnacles and mussels species such as limpets or goose barnacles occurred in the field in relatively small amounts at all sites; on 'Saddlebag Island' goose barnacles did not occur at all. Other potential prey species (the predatory snail *Nucella* and chitons) were extremely rare at all sites.

#### *Diet composition*

At all sites barnacle spp. and mussels were the main two prey species in the diet of *Pisaster* (see Figure 5 and Appendix 3b). The proportion in which the two types of prey occurred in the diet differed strongly per study site. At two sites, 'Saddlebag Island' and Neah Bay, starfish were mainly preying upon barnacles (more than 80 % of their diet), while at 'Clallam Bay' and North Island, and 'Strawberry Draw' and 'Simon's Landing' barnacles occurred in the diet in respectively less than 50 and 20 % of the time respectively. At these sites mussels instead of barnacles were most important prey for *Pisaster*. Starfish at the three sites on 'Tatoosh' had about 60 % or more mussels in their stomachs. At the two mainland sites the percentage of mussels in the diet was less than that.

At all locations where mussels of both species (*M. californianus* and *M.trossulus*) occurred together, *Pisaster* more often consumed *M.californianus* than *M. trossulus*. At 'Saddlebag Island' where only *M.trossulus* occurred, the mussels were found in small amount in *Pisaster*'s diet.

Goose barnacles occurred in fair amount in *Pisaster*'s diet. At almost all the sites where goose barnacles occurred (thus not at 'Saddlebag Island' and Strawberry Draw) the species were found for about 10 % in the diet of starfish; only at 'Neah Bay' starfish consumed them less. They were not consumed in the boulder field of Strawberry Draw, where they did not occur.

Species like limpets, *Nucella* and chitons were rarely observed in the diet at almost all sites. Only in the boulder fields of 'Strawberry Draw' did starfish consume chitons in fair amount (more than 10 % in their diet). Some species (herbivores snails and crabs (see appendix) were observed even more rarely in the diet. The availability of these species in the field was not measured in the field.



### *Food preference*

The preference of starfish for certain prey species differed slightly between sites (Figure 6 and Appendix 3c). Starfish at all but one site preferred mussels of both *M. californianus* and *M. trossulus* above all other species. Only at 'Simon's Landing' starfish did prefer *M. californianus*, but avoided *M. trossulus*. Although abundant in the field, barnacles were either avoided by starfish or consumed in proportion to their abundance.

The food preference of *Pisaster* for less abundant prey differed between site. Goose barnacles, *Nucella* and chitons were highly avoided at some sites, while at other sites they were tolerated or even preferred. Limpets were the only prey that was highly avoided by starfish of all sites. *Pisaster* avoided the herbivore snail *Tegula* that only occurred in the boulder field of Strawberry Draw.

### **Length categories within prey species**

#### *Food availability in field*

To know more accurately what length of prey *Pisaster* preferred, some prey species were subdivided into length categories. Per length categories prey availability and diet composition of starfish were obtained in the field. At 'Saddlebag Island' and 'Neah Bay' the abundant barnacle population mainly consisted of small individuals, while at the other sites the barnacle population consisted mainly of large individuals or both length categories occurred in similar proportion (Appendix 3a).

Mussel beds of *M. californianus* consisted mainly of medium sized individuals at all sites. Large individuals could occur in less, but fair amount, while mussels of the smallest length category relatively rare (Appendix 3b).

All length categories of chitons were extremely rare in the field of all sites.

#### *Diet composition and food preference*

At 'Saddlebag Island' and 'Neah Bay' starfish mainly preyed upon small sized barnacles, whereas starfish at other sites preyed mainly upon the larger barnacle individuals (Figure 7 and Appendix 3c). Only at 'North Island' *Pisaster* took barnacles of both length categories of barnacles in same amount. At all sites starfish preyed upon barnacles in correlation to their abundance or less than that.

Starfish differed in their choices of a specific length category of mussels. At Clallam Bay, 'Simon's Landing' and in the boulder field of Strawberry field *Pisaster* preyed mainly upon the large individuals, while at the other site at 'Strawberry Draw' and 'North Island' more medium sized mussels were consumed. Only at 'Neah Bay' *Pisaster* took medium and large sized mussels in equal amount. Small mussels rarely occurred in the diet of all starfish.

*Pisaster* rarely preyed upon chitons. Only in the boulder field of 'Strawberry Draw' starfish consumed some chitons in relative fair amount. The starfish selected thereby only large chitons.

### **Interaction strength**

Per capita interaction strength and species impact of *Pisaster* on the prey community were calculated for the study sites 'Saddlebag Island' and 'North Island' only (see Figure 8). On 'Saddlebag Island' where only a few prey species of *Pisaster* occurred, *Pisaster* had large per capita effect on mussels *M. trossulus*, and less on barnacles (Figure 8a). No effect was detected of starfish on other species, such as

limpets and chitons in the benthic community. On 'North Island' *Pisaster* had a large per capita effect on mussels, both species, but largest on *M. trossulus*. An intermediate per capita effect of *Pisaster* was detected for goose barnacles, while only a small per capita effect could be detected on populations of barnacles, chitons and *Nucella* spp. On 'North Island' starfish had no effect on the limpet population.

At both sites the per capita effect of *Pisaster* on the individual of a prey species was largest for the large individuals of the prey population (Figure 8b); except for the chiton population on North Island. Here *Pisaster* only preyed upon medium sized chitons, and therefore influenced only this length category within the chiton population.

Species impact of the predator population on the prey community at both sites was smaller than the per capita effect of the starfish, as density of the starfish was less than one individual per square meter (Figure 8c).

In comparing the effect of starfish on prey population at 'Saddlebag Island' with that on North Island, *Pisaster* had an overall larger effect on prey species on North Island. Differences were only slight for barnacles, but starfish had twice as large effect on *M. trossulus* on 'North Island' and Saddlebag Island.

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## Discussion

### The relation between *Pisaster* and its prey

*Pisaster ochraceus* has a wide range of occurrence; from Alaska to California (Ricketts and Calvin 1952). Along this range the starfish are exposed to different environmental conditions. The Strait of Juan de Fuca, where along the study sites are located, is only a small area within the large range at which *Pisaster* occurs. But even on this scale *Pisaster* experienced differences in environmental factors (Harley 1998). Despite these environmental differences among sites, *Pisaster* occurred at all these sites in fair amount. At five of them even in similar density (Figure 1a). The average density of *Pisaster* at these five sites was less than one individual per square meter. At the sixth site, 'Simon's Landing' starfish were twice as abundant as at the other sites with 1.5 individuals per square meter. The data agree with results of Paine (1976) and Robles *et al.* (1995). Paine found at sites along the NW Pacific coast densities of *Pisaster* ranging from  $<0.02$  to  $>2$  individuals per square meter. He was not able to explain differences in density among sites, neither am I. By measuring specifically the environmental parameters at the study sites, differences between the four study sites concerning predator density and other characteristics could have been explained or at least better understood. The lack of these data in this study can be seen as an error in the design.

Starfish populations at the six sites differed in their mean body size (Figure 1b). Starfish at 'Saddlebag Island' were significantly smaller (about 5 centimeter) than the ones at the other sites. Body size of *Pisaster* is determined by indeterminate growth influenced by age of the organism, but also by environmental factors. Paine (1976) found a negative relation between size of starfish and density of occurrence. This suggests that starfish are able to adjust their body size to the environmental circumstances, here predator density. However, in this study, at the site where starfish density was highest (Figure 1a), the starfish were certainly not smallest size (Figure 1b). At 'Saddlebag Island' were starfish were significantly smaller, the starfish occurred in same densities as the larger starfish of four other sites. Therefore differences in starfish density is not likely to provide an explanation for differences in starfish size in this study.

Feeding activity of starfish may be dependent on environmental factors as water temperature and wave action. Feeding activity is positively related with water temperature (Sanford 1999), but negatively related with wave action (Menge *et al.* 1996). Throughout a year both temperature and wave action are changing; in fall temperature is decreasing, while wave action increases. Therefore feeding activity is depending on season (Sanford 1999). The starfish population differed in feeding activity among the sites (Appendix 2). The differences in feeding activity of starfish at the three sites on 'Tatoosh' Island might be due to seasonal changes. 'North Island' was sampled at the begin of the summer (June and July), while 'Simon's Landing' was sampled at the end of the summer (September).

Differences in feeding activity of starfish of 'Tatoosh' and the other three sites could also be explained by differences in environmental factors as water temperature and wave action. 'Tatoosh' Island is located at the western entrance of the Strait, where the rocky shores of the island are wave exposed throughout the year. Saddlebag Island, however, is located at the eastern terminus of the Strait, in the protected waters of the Fuca-Georgia-Puget Basin. As wave action negatively influenced the feeding activity of starfish (Menge *et al.* 1996), feeding activity of starfish is expected to



increase along the west-east line along the Strait. In contrast with these expectations feeding activity of *Pisaster* at 'Saddlebag Island' was lower than that of starfish at the two mainland sites, and, surprisingly, similar with the activity of starfish at Tatoosh. The unexpected low feeding activity of starfish on 'Saddlebag Island' could be caused by a sampling error. On 'Saddlebag Island' starfish consumed particularly small prey individuals, smaller than the ones starfish at the other study sites preyed on (Figure 2). It is expected that digestion time of prey by *Pisaster* is dependent on prey size. A starfish will need less time to digest a small individual than a large one. It may take a starfish less than a tide to digest small prey individuals, while they may need more than one tide to digest large prey individuals. In this study diet composition of *Pisaster* was obtained during periods of low tide. This method of measurement might be sufficient to detect diet composition and feeding activity of *Pisaster* at the study sites where mainly large prey individuals were consumed. This method however, could be too coarse to reveal feeding activity for starfish mainly feeding upon small prey as the ones on Saddlebag Island. On the other hand the method used could also give an overestimation of the feeding rate of starfish eating large prey. Thus that the feeding activity of starfish at the sites other than 'Saddlebag Island' is lower than calculated here. I think that this will not give a satisfied explanation for the differences in feeding activity, as starfish were only rarely observed consuming prey individuals longer than 5 cm (personal observation).

Although prey availability for *Pisaster* differed among the sites (see Figure 4 and Appendix 3a)), food preference of starfish turned out to be quite similar among sites (see Figure 6 and Appendix 3c)). *Pisaster* seemed to have an overall preference of mussels and an overall avoidance for limpets. Only at 'Simon's Landing' starfish avoided blue mussels *M. trossulus*, probably because the prey species was extremely rare at this site. Barnacles were either avoided by *Pisaster* or taken in correlation to the abundance of the barnacle population. The results of this study are in accordance with results of earlier studies (Landenberger 1986; Paine 1966). The electivity index was quite sensitive for rarely occurring prey species. When calculating the index with only small number of data, slight differences in number (0 or 2) could change the index considerably (see Appendix 4). This could explain the variability of *Pisaster*'s preference for prey species as chitons and *Nucella spec.*. These species did rarely occur in the field and in *Pisaster*'s diet. To use the index reliable and to prevent misinterpretation of this index, a minimum number of data should be collected or attention should be focus on more common prey species.

Starfish seem to have a higher preference for the longer length categories than for the smallest ones within a prey species (Figure 7). Consumption of extremely long prey individuals was rarely observed in *Pisaster*'s diet. It seems that starfish try to prey upon an optimal length of prey. As small individuals will take little time to open, but will give just little energy in return, these prey will be avoided. Extremely large individuals, on the other hand, might give a lot of energy, but take long time and much energy to open. The length category were of prey were cost of opening and benefits of energy is optimal, should be the best prey to prey on. This might explain the preference of *Pisaster* for the largest length category of mussels ( $\geq 3$ )(see Figure 7) with mean size of 3.5 cm long mussels (see Figure 2).

Differences in size and thus energy content could be a reason why also between species, *Pisaster* has most preference for larger species as mussels and chiton and less for small ones as barnacles (Figure 6). On nutritional basis small barnacles are about one-third of large mussels and chiton (Paine 1966), and thus barnacles should be less preferred by *Pisaster* as shown in figure 6. However, this can not

explain why limpets are avoided. Perhaps these species are able to attach so firmly to the rock surface, that although they would have been attractive for their energy content (benefits) it takes *Pisaster* too much energy before getting it (costs).

It is interesting to see that *Pisaster* populations occurred at all six sites, although there are certain differences in food availability and in composition of preferred food among sites. At 'Saddlebag Island' and 'Neah Bay' the majority of the prey community consisted of only small barnacles. The prey community at 'Saddlebag Island' is rather poor with no real alternative prey species occurred besides barnacles (Appendix 3a). Individuals of the preferred prey, mussel *M. trossulus* did occur, but were extremely rare in the field; only in some refuges they were observed in some amount. Also at 'Neah Bay' barnacles were the numerically most abundant prey species, but at this site also other prey species did occur as beds of *M. californianus* (Figure 4). Starfish at both locations mainly preyed upon small prey individuals (as small barnacles), while the ones at the other four locations were mainly preying upon large individuals (medium and large sized mussels). The starfish of the first two populations were smaller than the ones at the latter four populations. As starfish are able to adjust their body size to the circumstances, it could be that the differences in body size could be explained by the differences in the composition of the prey community. Feder (1970) indicates that starfish mainly feeding on barnacles are smaller than those living on mussels are. The starfish at 'Saddlebag Island' and 'Neah Bay' may have adapted their body size to the available prey species of probably low food quality (barnacles) and are therefore smaller than the ones of the other sites. However this does not explain differences in size between the two populations at 'Saddlebag Island' and Neah Bay. Paine (1974) indicated that *Pisaster* do not attain large body sizes when there is strong competition for their food. Although the density of starfish was similar for both places, it could be that the competition for food between the starfish on 'Saddlebag Island' is stronger than at Neah Bay. A high amount of only small prey items is present at Saddlebag Island, while at 'Neah Bay' there is also more alternative prey species present beside the numerous numbers of small barnacles.

The marine predator had only a per capita effect upon two species, barnacles and mussels, of the prey assemblage on Saddlebag Island. The per capita effect of starfish on the mussel population was stronger than on the barnacle population, although the mussels were rare in abundance, suggesting that they were eaten preferentially. Other prey species as limpets were ignored. On 'North Island' *Pisaster* also had strongest effect upon the mussel population of the rock assemblage, especially the more rare mussel species *M. trossulus*. Within length categories *Pisaster* had stronger effect upon the medium and large sized individuals of the *M. californianus* mussels, which is a suggestion that *Pisaster* prey preferentially on these sized mussels.

Comparing the per capita effect of *Pisaster* on prey species occurring at both locations, the effect of *Pisaster* on *M. trossulus* was stronger for the prey population on 'North Island' than for the one on 'Saddlebag Island' (Figure 8a). On 'Saddlebag Island' no real beds of mussels occurred, but the mussels that occurred were small and almost undetectable hidden in the algae. Their number per square meter was surprisingly high. At 'North Island' *M. trossulus* were larger, but occurred in less amount. The effect of predation by *Pisaster* could therefore have a stronger impact on the *M. trossulus* population of 'North Island' than on the one of Saddlebag Island.



Navarrete and Menge (1996) measured the per capita effect of *Pisaster* on mussels *M. trossulus* using the experimental approach. They found a much stronger predation effect of *Pisaster* on the mussel population. Compared with their result, *Pisaster* would merely be a weak predator instead of a keystone species. The differences in results could be explained by uncertainties in the calculation of the per capita interaction strength in this study. Lack of accurate measurements on daily feeding rate of *Pisaster* on certain prey species made it necessary to estimate a consumption rate. For some prey species, especially the small ones, the estimated feeding rate of *Pisaster* might be an underestimation of the actual feeding rate. The actual per capita effect could be higher than estimated here. Another reason could be that the food availability of prey species in the field is measured in a broader range than *Pisaster* actually feed in. Starfish might stop directly at the edge of a mussel bed to forage there, while in this study mussels and other prey species in the lowest half-meter of the bed were also taken as potential prey of *Pisaster*.

It could also be that the per capita effect Navarrete and Menge calculated in their study (1996) is an overestimation of the reality. The experimentally transplanted mussels were allowed to a location low in the intertidal. As starfish would easily come that high upon the shore, the resulted per capita effect might be stronger than when the mussels were transplanted to a location higher in the intertidal.

### Methods of measurement

The data collection methods in this study had some drawbacks. First, at some study sites two types of habitat occurred; rocky bench and boulder field. The method used to measure food availability was appropriate for the bench habitats, but not for the boulder field habitats. At each site, prey densities were measured separately in 2, 3 or 4 intertidal zones. These zones were readily distinguished on the more or less two-dimensional surfaces of rocky benches. Boulder fields, however, are three-dimensional habitats in which zone extends both vertically up the rock and horizontally out from the shore. Measuring the food availability in a three dimensional space is more complicated; in this study not much attention is paid to develop an accurate way to evaluate prey accessibility in these habitats. Food availability on one rock could be measured as accurate as it would be measured on a bench. The difficulty will be how to determine these values for the whole boulder field.

Second, not all habitat types in the total study area were sampled. Vertical walls surrounded by surge channels, where *Pisaster* may be abundant, were not sampled. Third, sites with low starfish densities were not sampled. Similarly, within sites, benches with low starfish densities were not sampled. If *Pisaster* aggregated at the best food locations, the actual food availability of the total study site could be less than the calculated one.

### The observational approach

When organisms are large and / or highly mobile it may not possible to use experiments to quantify relations between species (Wootton 1997). In this case an approach in which only observations are required has a strong advantage. When studying shorebirds foraging on the intertidal community, Wootton (1997) was able to use such an observational approach. In the following paragraphs the problems of the observational approach as encountered in this study on *Pisaster* – prey communities are discussed.



### Feeding rate

Species impact was calculated with the formula used by Wootton (1997):

$$SI = -\rho\phi(1/\delta)\lambda\beta,$$

In this study assumptions were made in calculating all parameter values. One of the least well-known parameter values was the consumption rate of *Pisaster* ( $\rho$ ), which is defined as the mean number of prey consumed per eating starfish per time. Some data were available for the feeding rate of *Pisaster* on 3 to 4 cm large mussels, but the feeding rate on other species or other size categories of mussels was unknown. Based on field observations of Paine (1969) I assumed the daily feeding rate of starfish on prey other than large mussels as twice (two tides in a day) the number of prey found in the starfish's stomach divided by the number of foraging predators. This assumption could be true for some prey individuals, but not for all of them. The rate of feeding will not be constant for all prey individuals; for instance, it is likely to depend on prey length (smaller individuals will be digested more easily than large individuals). *Pisaster* may need less than one tide to consume small prey, while it may need more than a day or even two days to consume one large mussel. Thus the assumed feeding rate of *Pisaster* on small prey could be an overestimation, while it could be an underestimation for large prey. Furthermore the assumed feeding rate of *Pisaster* does not take into account difference in predator sizes. Large starfish tend to prey upon larger prey individuals (Paine 1974) and therefore feeding rate may differ between starfishes of different sizes. Species impact can be calculated more accurately when the feeding rate of *Pisaster* on several prey species in different size categories is measured. Thus further experiments on feeding rate of *Pisaster* are required to improve the observational approach.

### Feeding activity

A parameter that is closely related to the feeding rate of *Pisaster* is the fraction of the starfish population that was feeding in the field ( $\phi$ ). This proportion depends on several environmental characteristics such as temperature, wave action, tide and season. Feeding activity is for instance positively influenced by water temperature (Sanford 1999), but is negatively influenced by wave action (Navarrete and Menge 1996). Moreover feeding activity of starfish has also been shown to be twice as high during high tide as during low tide (Robles *et al.* 1995). In this study feeding activity is only measured during low tide. Differences in environmental factors between or within sites are not taken into account and therefore may have confounded the results. Further experiments are required to clarify the importance of environmental factors on the *Pisaster* – prey community.

### Prey availability

The number of prey available ( $\delta$ ) to *Pisaster* was observed in the field by counting the number of prey in a quadrat and extrapolating this number to a square meter. Measuring the number of prey is an easy and quick method to get an idea of prey availability. However, counting numbers one assumes that 'numbers' triggers *Pisaster*'s feeding behavior. Prey availability however can also be expressed in other currencies (e.g. energy contents). Barnacles are known to be numerically the most abundant prey, but to contain less than one-third of the energy value of a mussel or a chiton. Both mussels and chitons are known to be preferred by *Pisaster* over barnacles. It would be interesting for further research to determine whether interaction strength depends on the currency used to express prey availability.

### Time available for feeding

The proportion of time the prey community on the rocky shore was available for *Pisaster* ( $\lambda$ ) was assumed to be one, as the digestion of prey continues. *Pisaster*'s feeding behavior is, however, known to be influenced by the tidal cycle. With upcoming tide *Pisaster* moves up the shore to prey upon the benthic community, while with out- going tide the starfish retreats into cracks and surge channels in the low intertidal for protection from desiccation (Robles *et al.* 1995). Thus starfish can actively forage during high tide, but not during low tide. Therefore  $\lambda$  is likely to be lower than one. The observational approach will become more operational when the exact value of  $\lambda$  is determined.

### Predator density

Measurements of *Pisaster* density ( $\beta$ ) were made during low tide, when starfish retreat to the lower part of the shore. Only starfish positioned above the low water line could be observed. As it is likely that a part of the starfish population remained under water, the actual predator density is likely to have been higher than the measured density.

## Conclusions

The observational approach is not yet applicable for the study of *Pisaster* – prey communities. Before an observational approach can be used, more information is needed on several parameters involved:

- Feeding rate
- Feeding activity
- Prey availability
- Time available for feeding
- Predator density

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Theunis Piersma is the person who gave the start to this project, I would like to thank him for that.

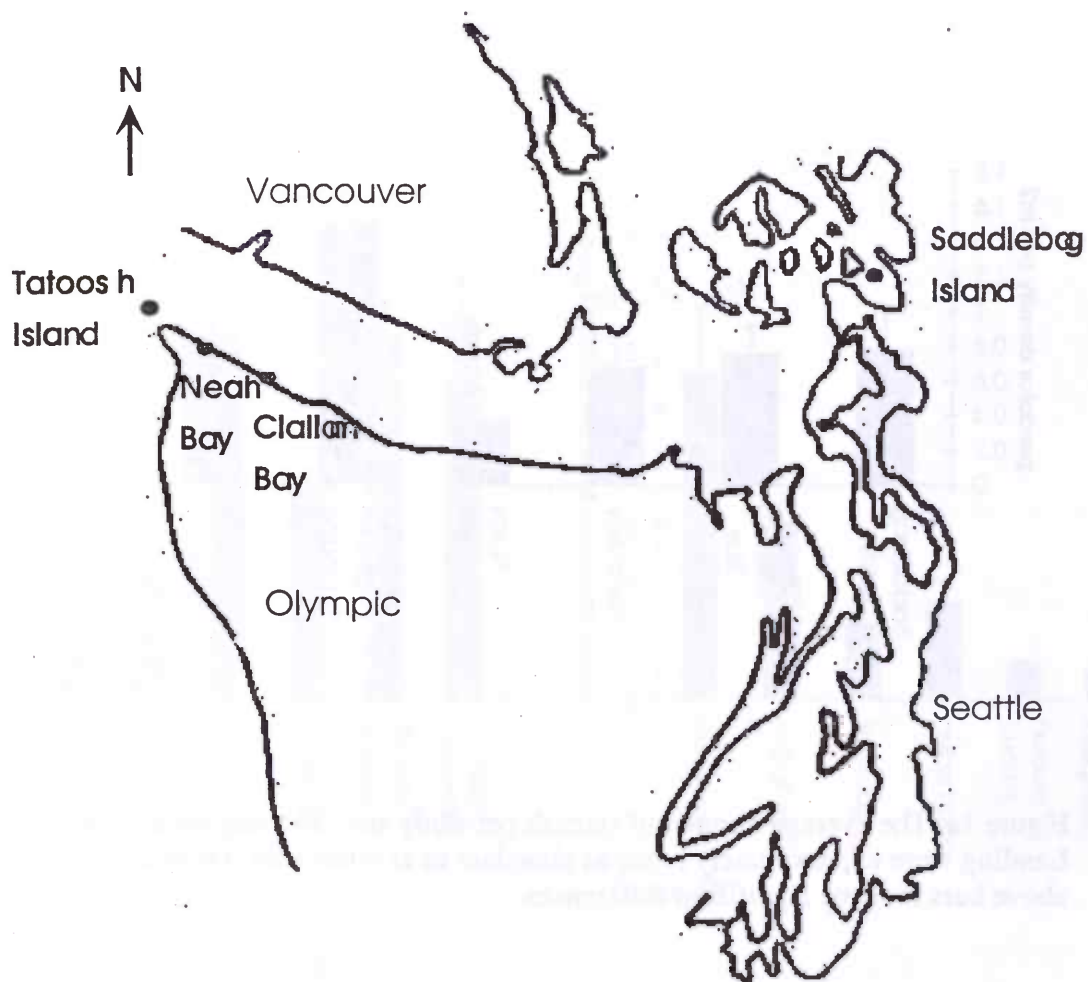


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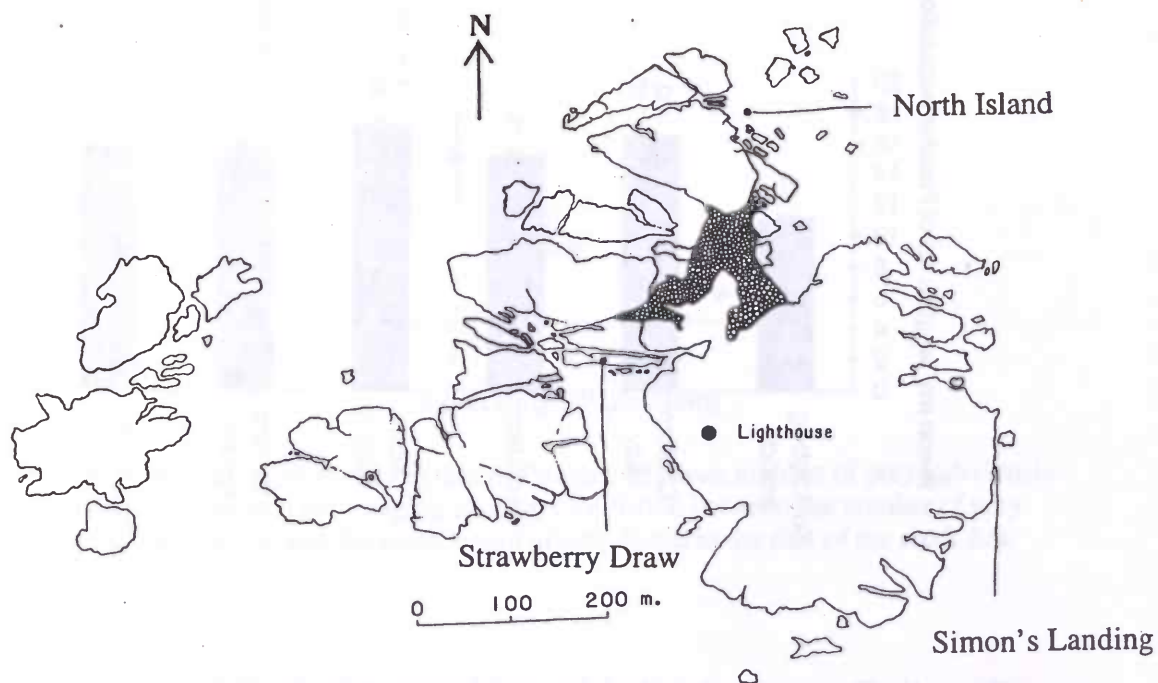
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Picture 2a: The four study sites along the Strait of Juan de Fuca: 1 'Tatoosh'; 2 'Neah Bay'; 3 'Slip Point' and 4 'Saddlebag Island'.



Picture 2b: The three study sites on site 1 'Tatoosh': 1a 'North Island', 1b 'Strawberry Draw', and 1c 'Simon's Landing'.



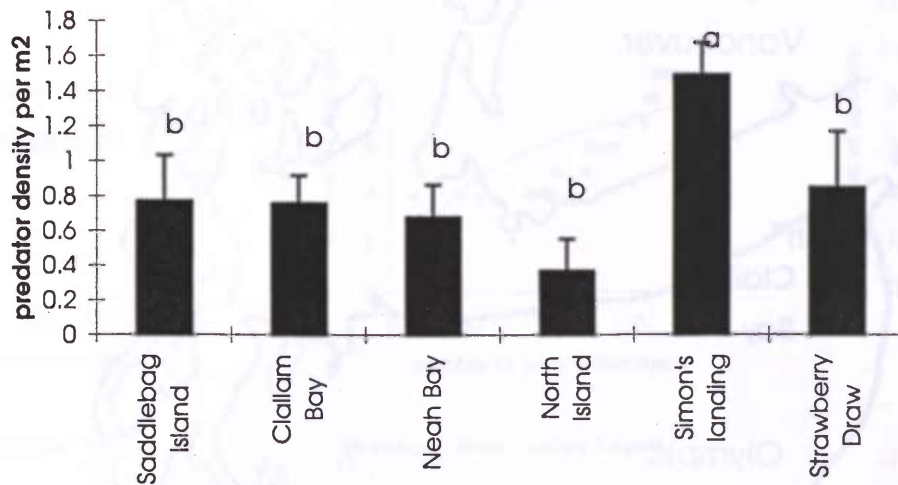


Figure 1a: The average number of starfish per study site. The starfish at Simon's Landing were approximately twice as abundant as at other sites. Different letters above bars indicate significant differences.

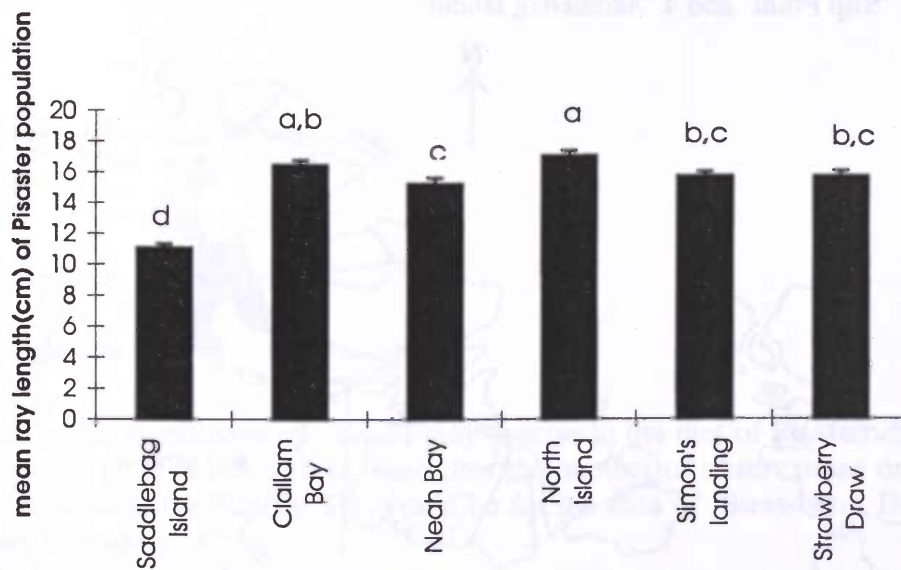


Figure 1b: The mean ray length of the starfishes per study site. Different letters above bars indicate significant differences.

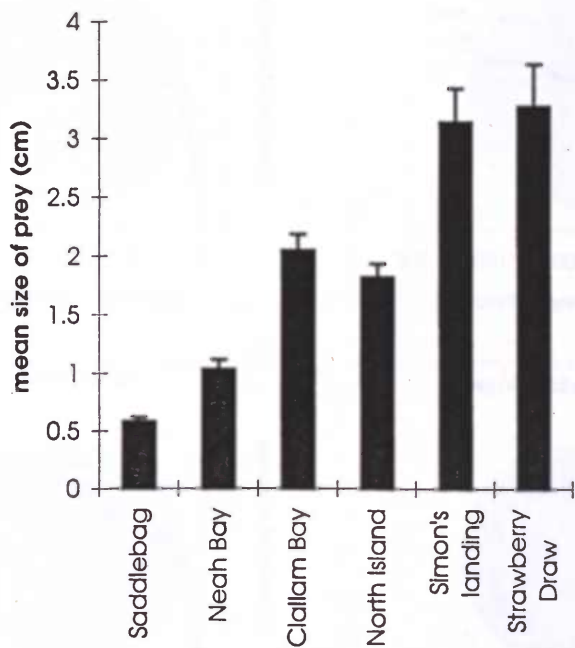


figure 2a

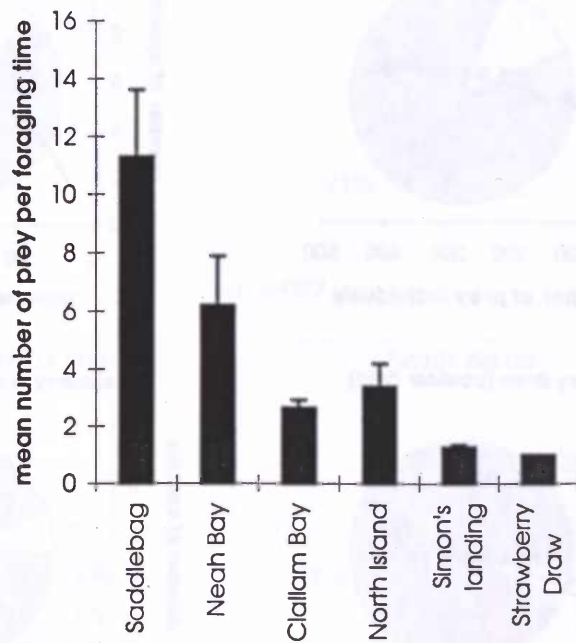


figure 2b

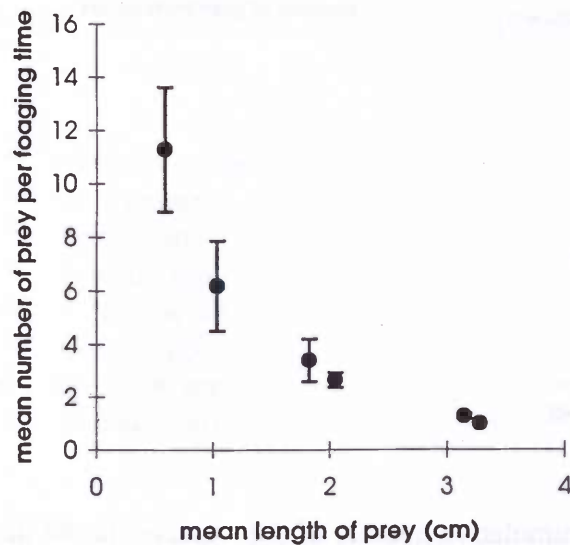


Figure 2: a) Mean size of prey found in diet of *Pisaster*; b) Mean number of prey individuals found in *Pisaster*'s stomach per foraging attempt; c) Relation between the number of prey individuals in the stomach and the mean length of prey found in the diet of the starfishes.

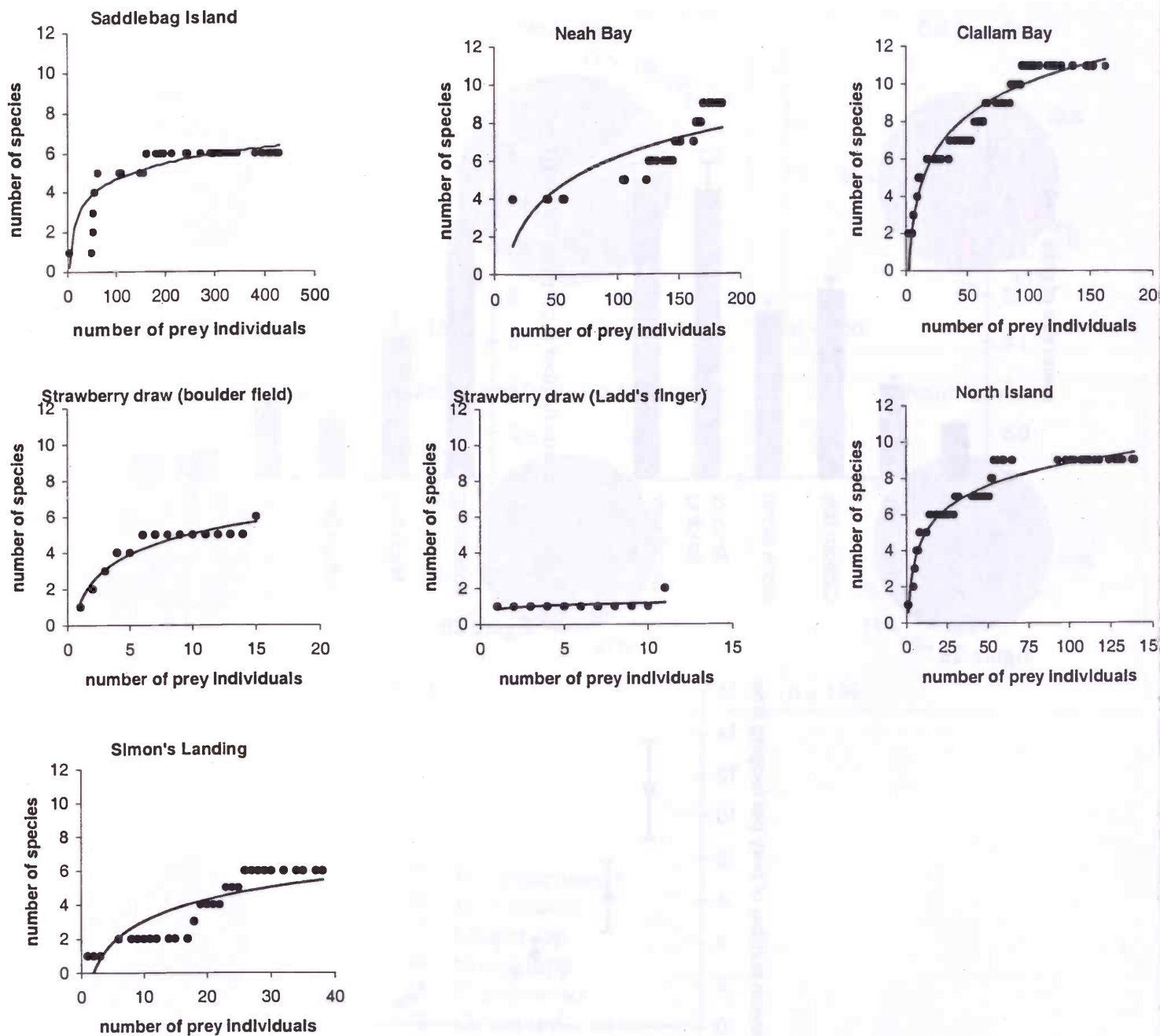


Figure 3: The cumulative number of prey species in the diet of *Pisaster*. Not in every site an asymptote is reached: in these sites the number of observations on the diet of the starfish was insufficient. This could be for the data of 'Strawberry Draw' and of 'Simon's Landing'.



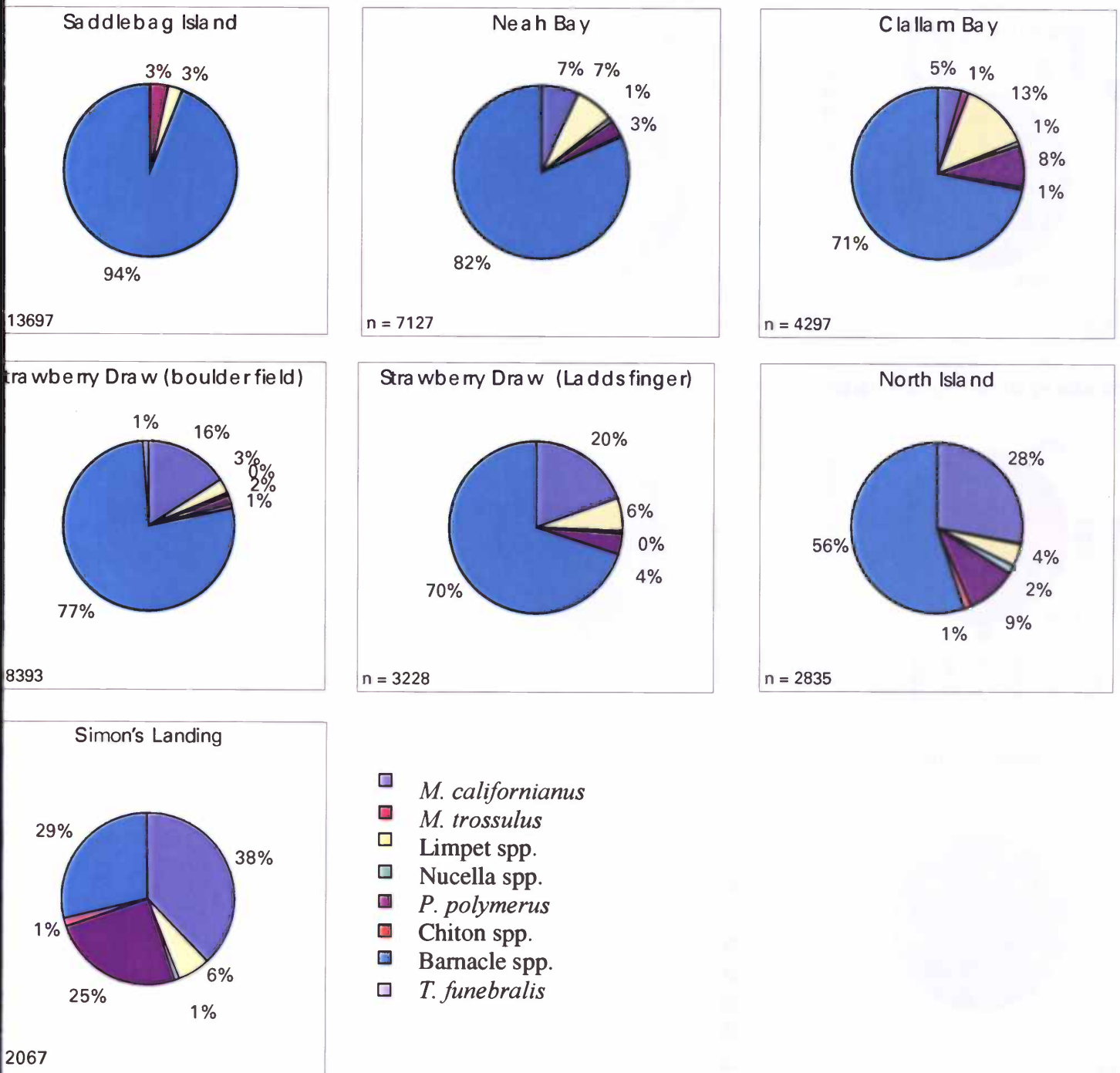


Figure 4: Percentage of prey species of total prey assemblage observed in the field per study site. Barnacles were abundant at all the sites, mussels (mainly *M. californianus*) only at the four sites on Tatoosh. Limpets and goose barnacles occurred in fair amount at some sites.

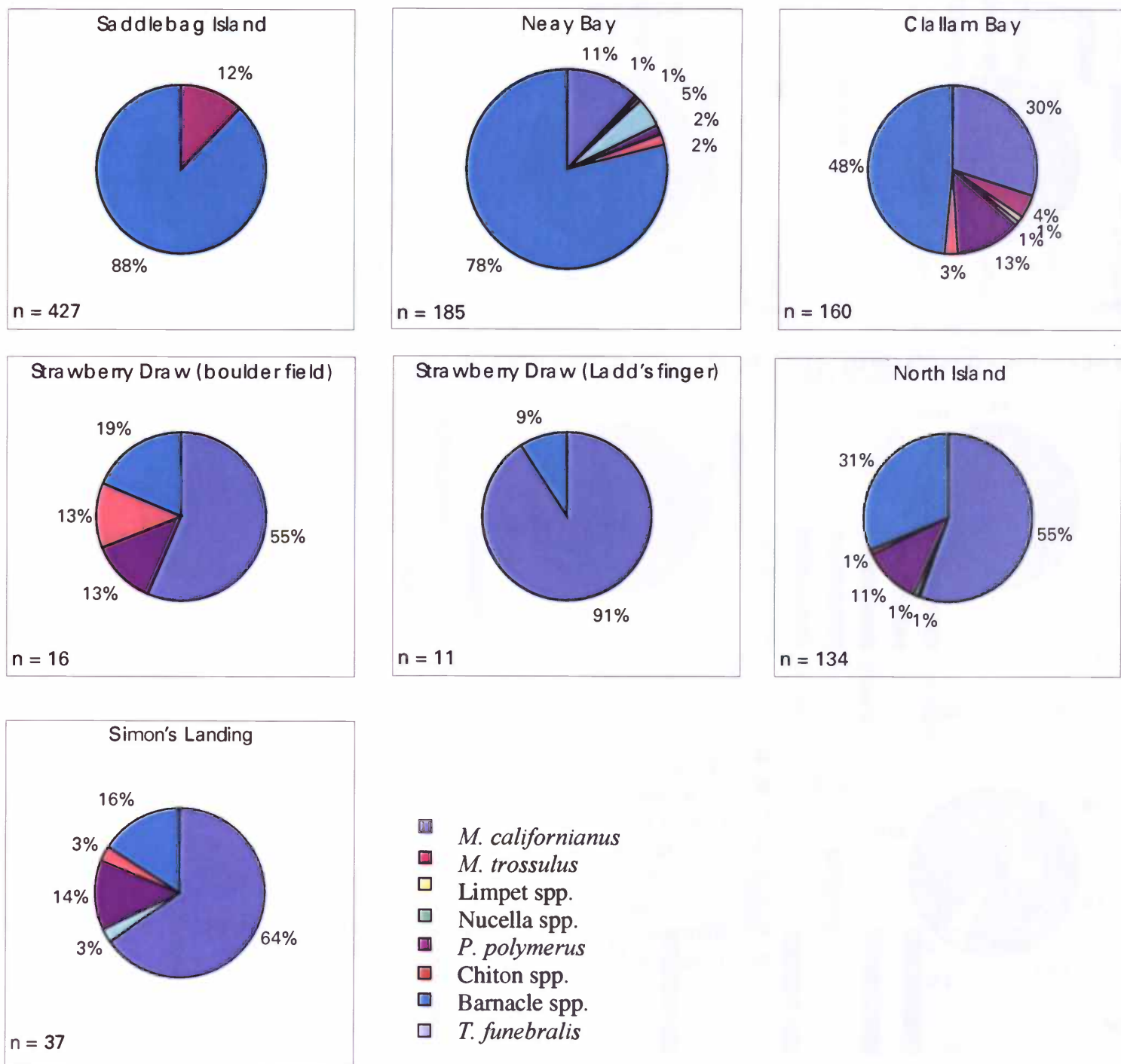


Figure 5: Percentage of prey species of total prey assemblage observed in the diet of the starfish per study site. Barnacles were abundant in the diet of starfish at the sites other than on 'Tatoosh'. On 'Tatoosh' they occurred in fair amount in *Pisaster*'s diet. Starfish at 'Tatoosh' were found with a high percentage of Mussels *M. californianus* in their diet. Starfish of the six sites were variable in their consumption of goose barnacles, chitons and *M. trossulus*.

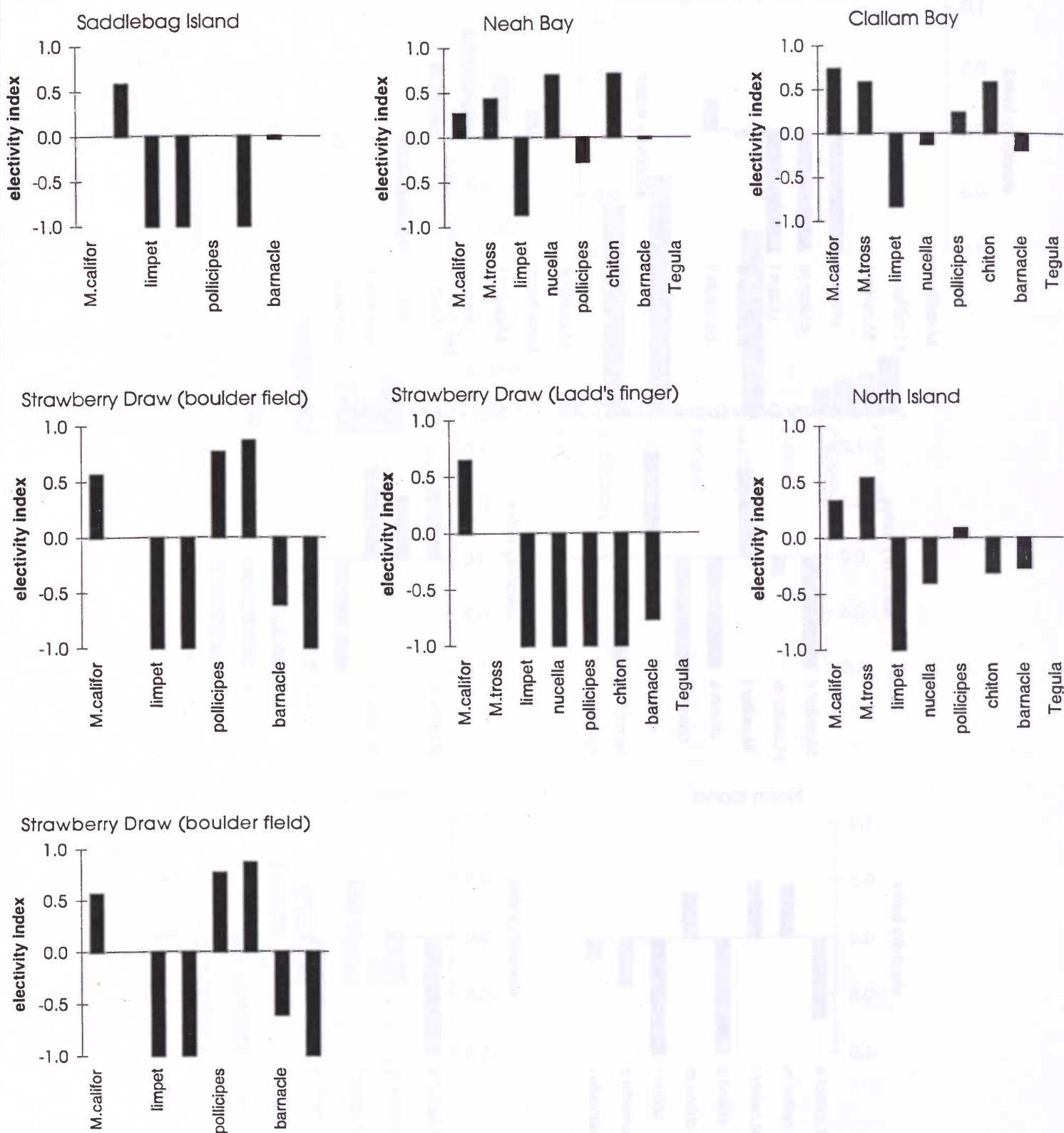


Figure 6: Food preference of starfish for prey species per study site. *Pisaster* had a strong preference of both mussels species. Barnacles were either avoided or consumed in relation to their abundance, limpets were avoided by starfish of all sites. The starfish was variable in their preference for the more rare prey species.



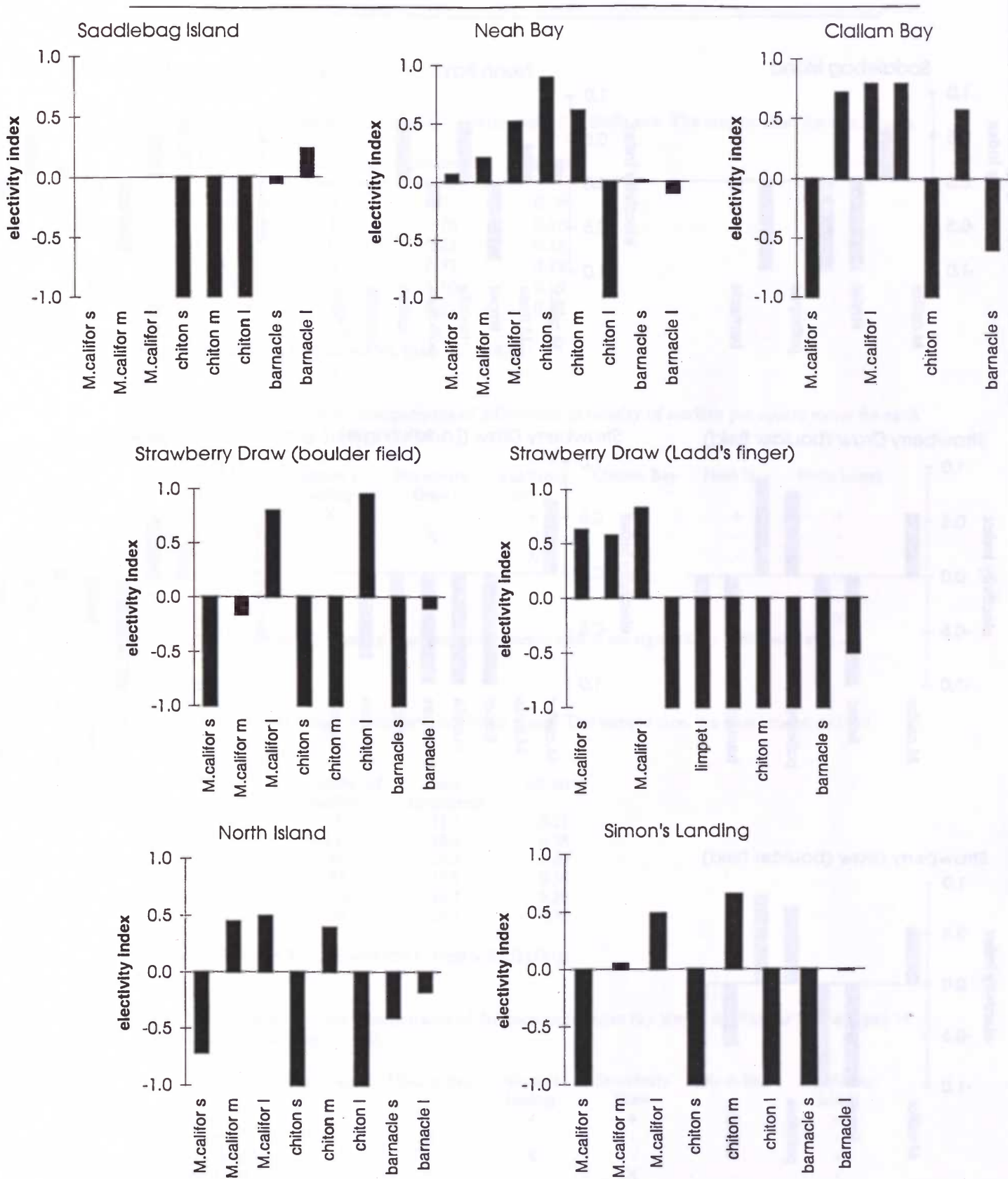


Figure 7: Food preference of starfish for different length categories of prey species per study site. *Pisaster* preferred the longer prey individuals more than the smaller ones.

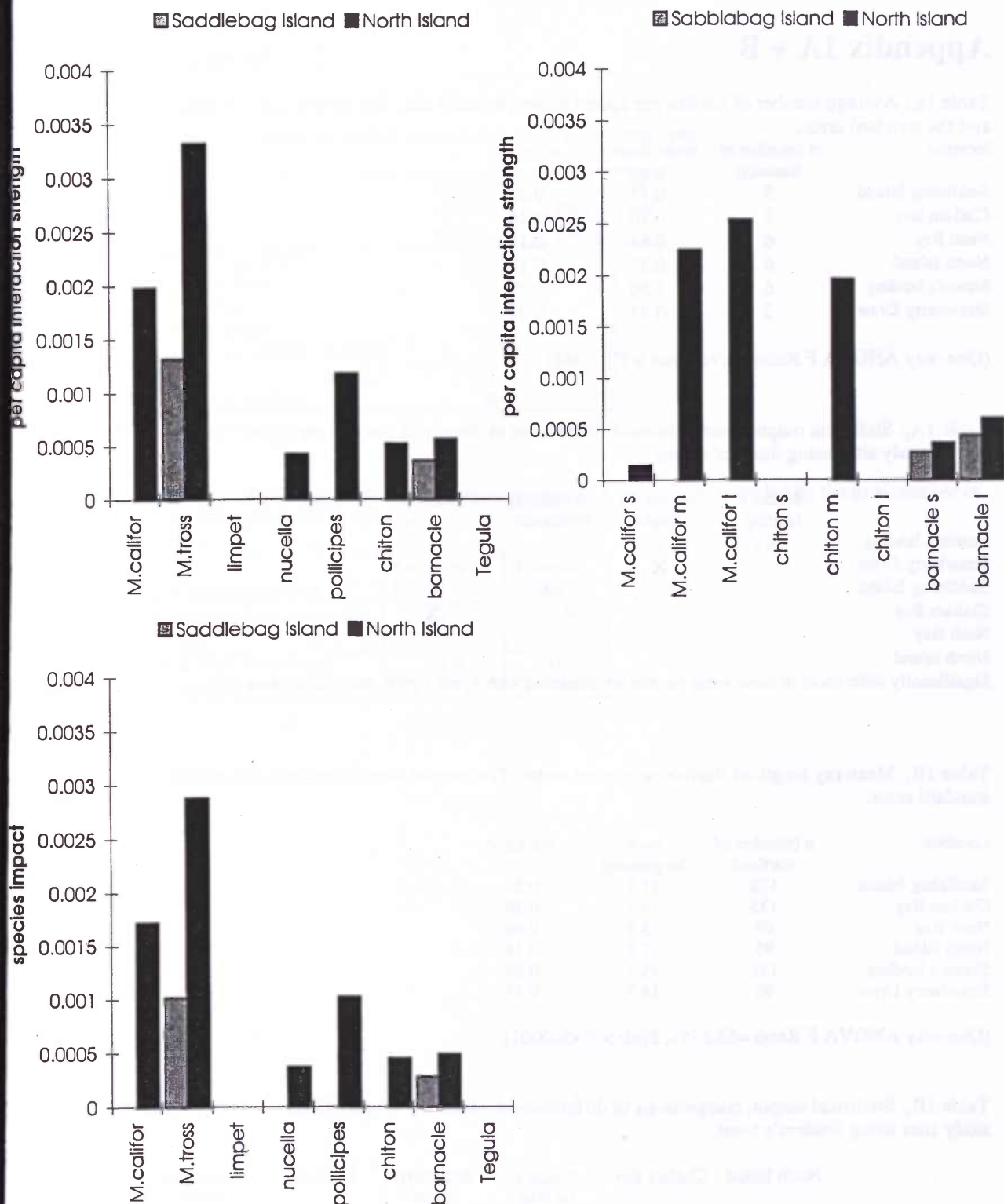


Figure 4.8: a) Per capita interaction strength of *Pisaster* on prey species and b) on length categories within prey species, and c) species impact of the starfish population on the prey population. *Pisaster* had strongest effect on the mussel population and within the mussel population on the largest mussels. Starfish on North Island had a stronger effect upon the mussel population than the ones on Saddlebag Island. Species impact of *Pisaster* on the prey population was smaller than the per capita effect.

## Appendix 1A + B

Table 1a<sub>1</sub>: Average number of starfish per square meter per study site. The sample size, the exact mean and the standard error.

location	n (number of transect)	mean density (cm)	std. error
Saddlebag Island	3	0.77	0.26
Clallam Bay	8	0.76	0.16
Neah Bay	6	0.68	0.19
North Island	6	0.37	0.19
Simon's landing	6	1.50	0.19
Strawberry Draw	2	0.85	0.32

(One-way ANOVA F Ratio =3.96, Prob > F 0.0088)

Table 1A<sub>2</sub>: Statistical output; comparisons of differences in density of starfish per square meter for each pair of study sites using Student's t-test.

	Simon's landing	Strawberry Draw	Saddlebag Island	Clallam Bay	Neah Bay	North Island
Simon's landing	X	-	+	+	+	+
Strawberry Draw		X	-	-	-	-
Saddlebag Island			X	-	-	-
Clallam Bay				X	-	-
Neah Bay					X	-
North Island						X

Significantly differences in mean value per site are presented with +; not significantly differences with -.

Table 1B<sub>1</sub>: Mean ray length of starfish per square meter. The sample size, the exact mean and the standard error.

Location	n (number of starfish)	mean length(cm)	std. error
Saddlebag Island	172	11.1	0.25
Clallam Bay	135	16.5	0.28
Neah Bay	69	15.2	0.40
North Island	95	17.0	0.34
Simon's landing	126	15.7	0.29
Strawberry Draw	90	15.7	0.35

(One-way ANOVA F Ratio =63.2551, Prob > F <0.0001)

Table 1B<sub>2</sub>: Statistical output; comparisons of differences in mean ray length of Pisaster for each pair of study sites using Student's t-test.

	North Island	Clallam Bay	Simon's landing	Strawberry Draw	Neah Bay	Saddlebag Island
North Island	X	-	+	+	+	+
Clallam Bay		X	-	-	+	+
Simon's landing			X	-	-	+
Strawberry Draw				X	-	+
Neah Bay					X	+
Saddlebag Island						X

Significantly differences in mean value per site are presented with +; not significantly differences with -.



## Appendix 2

Table 2<sub>1</sub>: Number of starfish eating and not eating per study site

	number of starfish eating	Number of starfish not eating
Saddlebag Island	38	131
Clallam Bay	66	53
Neah Bay	30	25
North Island	41	54
Strawberry Draw -boulder	15	45
-bench	11	22
Simon's landing	30	100

Table 2<sub>2</sub>: Feeding activity in percentage (number of eating starfish divided by the total number of starfish observed) for two study sites during during the season.

% feeding activity	Saddlebag Island	Tatoosh Island
summer (begin Aug/end July)	22.5	33.9
fall (end November/ begin September)	15.0	20.8

## Appendix 3

Table 3.: percentage of prey species of total prey assemblage observed in the field per study site.

% of prey species in field	Saddlebag Island	Clallam Bay	Neah Bay	North Island	Strawberry Draw (Ladd's)	Strawberry Draw (boulder)	Simon's landing
M.califor s	0.00	0.01	0.02	0.09	0.02	0.01	0.04
M.califor m	0.00	0.02	0.04	<b>0.13</b>	<b>0.15</b>	<b>0.09</b>	<b>0.19</b>
M.califor l	0.00	0.02	0.01	<b>0.06</b>	0.03	<b>0.06</b>	<b>0.15</b>
M.trossulus	0.04	0.01	0.00	0.00	0.00	0.00	0.00
limpet s	0.03	<b>0.10</b>	<b>0.06</b>	0.03	0.04	0.02	0.03
limpet l	0.00	0.03	0.01	0.01	0.02	0.01	0.02
Nucella spp.	0.00	0.01	0.01	0.02	0.00	0.00	0.01
P.polymerus	0.00	<b>0.08</b>	0.03	<b>0.09</b>	0.04	0.02	<b>0.25</b>
chiton s	0.00	0.00	0.00	0.00	0.00	0.00	0.00
chiton m	0.00	0.00	0.00	0.00	0.00	0.00	0.01
chiton l	0.00	0.01	0.00	0.01	0.00	0.00	0.00
barnacle s	<b>0.89</b>	<b>0.47</b>	<b>0.59</b>	<b>0.31</b>	<b>0.43</b>	<b>0.54</b>	<b>0.13</b>
barnacle l	<b>0.05</b>	<b>0.25</b>	<b>0.22</b>	<b>0.25</b>	<b>0.27</b>	<b>0.23</b>	<b>0.16</b>
Tegula	0.00	0.00	0.00	0.00	0.00	0.01	0.00

Table 3.: percentage of prey species of total prey assemblage observed in the diet of the starfish per study site.

% of prey species in diet	Saddlebag Island	Clallam Bay	Neah Bay	North Island	Strawberry Draw (Ladd's)	Strawberry Draw (boulder)	Simon's landing
M.califor s	0.00	0.00	0.02	0.01	<b>0.09</b>	0.00	0.00
M.califor m	0.00	<b>0.12</b>	<b>0.05</b>	<b>0.34</b>	<b>0.55</b>	<b>0.06</b>	<b>0.21</b>
M.califor l	0.00	<b>0.18</b>	0.04	<b>0.18</b>	<b>0.27</b>	<b>0.50</b>	<b>0.42</b>
M.trossulus	<b>0.12</b>	0.04	0.01	0.01	0.00	0.00	0.00
limpet s	0.00	0.00	0.00	0.00	0.00	0.00	0.00
limpet l	0.00	0.01	0.01	0.00	0.00	0.00	0.00
Nucella spp.	0.00	0.01	<b>0.05</b>	0.01	0.00	0.00	0.03
P.polymerus	0.00	<b>0.12</b>	0.02	<b>0.11</b>	0.00	<b>0.13</b>	<b>0.13</b>
chiton s	0.00	0.01	0.01	0.00	0.00	0.00	0.00
chiton m	0.00	0.00	0.01	0.01	0.00	0.00	0.03
chiton l	0.00	0.02	0.00	0.00	0.00	<b>0.13</b>	0.00
barnacle s	<b>0.81</b>	<b>0.12</b>	<b>0.61</b>	<b>0.13</b>	0.00	0.00	0.00
barnacle l	<b>0.07</b>	<b>0.36</b>	<b>0.18</b>	<b>0.17</b>	<b>0.09</b>	<b>0.19</b>	<b>0.16</b>
Tegula	0.00	0.00	0.00	0.00	0.00	0.00	0.00

Table 3.: Ivlev's electivity index per prey species per study site.

Ivlev's electivity index (E)	Saddlebag Island	Clallam Bay	Neah Bay	North Island	Strawberry Draw (Ladd's)	Strawberry Draw (boulder)	Simon's landing
M.califor s	-	-1.00	0.07	-0.72	<b>0.63</b>	-1.00	-1.00
M.califor m	-	<b>0.72</b>	<b>0.21</b>	<b>0.45</b>	<b>0.57</b>	-0.17	0.05
M.califor l	-	<b>0.79</b>	<b>0.51</b>	<b>0.49</b>	<b>0.82</b>	<b>0.80</b>	<b>0.49</b>
M.trossulus	<b>0.54</b>	<b>0.58</b>	<b>0.43</b>	<b>0.53</b>	-	-	-1.00
limpet s	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00	-1.00
limpet l	-1.00	-0.45	-0.28	-1.00	-1.00	-1.00	-1.00
Nucella spp.	-1.00	-0.13	<b>0.69</b>	-0.42	-1.00	-1.00	<b>0.44</b>
P.polymerus	-	<b>0.23</b>	-0.28	0.07	-1.00	<b>0.76</b>	-0.31
chiton s	-1.00	<b>0.79</b>	<b>0.89</b>	-1.00	-1.00	-1.00	-1.00
chiton m	-1.00	-1.00	<b>0.61</b>	<b>0.39</b>	-1.00	-1.00	<b>0.65</b>
chiton l	-1.00	<b>0.57</b>	-1.00	-1.00	-1.00	<b>0.95</b>	-1.00
barnacle s	-0.05	-0.60	0.01	-0.41	-1.00	-1.00	-1.00
barnacle l	<b>0.19</b>	<b>0.19</b>	-0.10	-0.17	-0.50	-0.10	-0.01
Tegula	-	-	-	-	-	-1.00	-



## Appendix 4

Table 4.: Species of rocky prey assemblage occurring in the field.

prey species in field	Saddlebag Island	Neah Bay	Clallam Bay	Tatoosh		
				North Island	Strawberry Draw	Simon's landing
mussels						
<i>Mytilus californianus</i>	-	x	x	x	x	x
<i>Mytilus trossulus</i>	x	x	x	x	-	x
acorn barnacles						
<i>Balanus glandula</i>	x	x	x	x	x	?
<i>Balanus nubilus</i>	-	x	x	x	?	x
<i>Chthamalus dalli</i>	x	x	x	x	x	x
<i>Semibalanus cariosus</i>	x	x	x	x	x	x
goose barnacles						
<i>Pollicipes polymerus</i>	-	x	x	x	x	x
chitons						
<i>Katharina tunicata</i>	x	x	x	x	x	x
<i>Mopelia</i> spp.	x	x	x	x	x	x
<i>Tonicella lineata</i>	x	x	x	x	x	x
other chitons	x	x	x	x	x	x
snails						
<i>Amphissa</i> spp.	?	?	?	x	?	x
<i>Ceratostoma mornatum</i>	?	?	x	?	?	?
<i>Littorina</i> spp.	?	?	?	x	?	?
<i>Nucella canaliculata</i>	?	x	x	x	x?	?
<i>Nucella emarginata</i>	?	x	x	?	x?	x
<i>Tegula funebris</i>	-	-	-	-	x	-
limpets						
<i>Lottia pelta</i>	?	?	x	?	?	?
other limpets	x	x	x	x	x	x
crabs	x	x	x	x	x	x

Table 4.: Species of rocky prey assemblage occurring in *Pissaster*'s diet.

prey species in diet	Saddlebag Island	Neah Bay	Clallam Bay	Tatoosh		
				North Island	Strawberry Draw	Simon's landing
mussels						
<i>Mytilus californianus</i>	-	x	x	x	x	x
<i>Mytilus trossulus</i>	x	x	x	x	-	-
acorn barnacles						
<i>Balanus glandula</i>	x	x	x	-	x	-
<i>Balanus nubilis</i>	-	x	x	x	-	x
<i>Chthamalus dalli</i>	x	-	-	-	-	-
<i>Semibalanus cariosus</i>	x	x	x	x	x	-
goose barnacles						
<i>Pollicipes polymerus</i>	-	x	x	x	x	x
chitons						
<i>Katharina tunicata</i>	-	-	x	-	x	-
<i>Mopelia</i> spp.	-	-	x	-	-	-
<i>Tonicella lineata</i>	-	-	-	-	x	x
other chitons	-	x	-	-	-	-
snails						
<i>Amphissa</i> spp.	-	-	-	x	-	x
<i>Ceratostoma mornatum</i>	-	-	x	-	-	-
<i>Littorina</i> spp.	-	-	-	x	-	-
<i>Nucella canaliculata</i>	-	-	-	x	-	-
<i>Nucella emarginata</i>	-	x	x	-	-	x
<i>Tegula funebris</i>	-	-	-	-	-	-
limpets						
<i>Lottia pelta</i>	-	-	x	-	-	-
other limpets	-	x	x	-	-	-
crabs	x	-	x	-	-	-