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PREDATION BY *Nucella lapillus* (LINNAEUS, 1758) ON *Littorina obtusata* (LINNAEUS, 1758) AND *Mytilus edulis* (LINNAEUS, 1758).

BY

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DISSERTATION

Submitted to the University of New Hampshire
in partial fulfillment of the
Requirements for the Degree of

Doctor of Philosophy

in

Zoology

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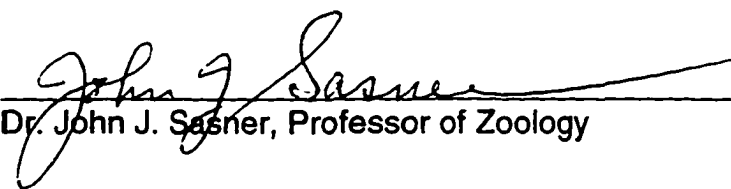
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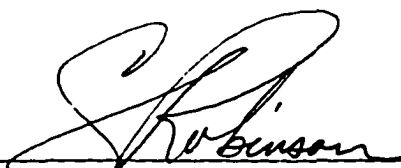
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ABSTRACT

PREDATION BY *Nucella lapillus* (LINNAEUS, 1758) ON
Littorina obtusata (LINNAEUS, 1758) AND *Mytilus edulis*
(LINNAEUS, 1758).

BY

Helena Matthews-Cascon
University of New Hampshire, May, 1997

Prey preference and recognition by individuals of *Nucella lapillus* from 13 different populations from New England were studied, to determine if individuals of this species kept on a single prey diet develops a preference for this prey, and if prey availability affects prey recognition in this predator. Individuals from all 13 populations showed a preference for *Mytilus edulis* over *Littorina obtusata* in laboratory experiments, including those from a population that prey only on *L.obtusata* in the field. Individuals from another population were not able to recognize *L.obtusata* as a prey. *N.lapillus* kept in a diet of *M.edulis* in the laboratory had its preference for this prey reinforced, but those kept in a diet of *L.obtusata*, did not develop a preference for this prey.

Adults and juveniles of *Nucella lapillus* showed higher feeding rates on both *M.edulis* and *L.obtusata*, in treatments with

higher prey density than in those with lower prey density. *Nucella lapillus* showed a higher growth rate feeding on *Mytilus edulis* than on *Littorina obtusata* during a 8 months laboratory experiment. The results indicate that *M. edulis* presented a greater "food value" for *N. lapillus* than *L. obtusata*.

Carcinus maenas appeared for the first time in obvious numbers in Pembroke, Maine in the summer of 1995. *C. maenas* is a predator of *N. lapillus*, and experiments were conducted to determine if *Nucella lapillus* from Pembroke, showed different predation rates on *Littorina obtusata* in the presence and absence of the green crab *Carcinus maenas*. Parallel experiments were also done using *N. lapillus* from Little Harbor, NH population, where the crab has been well established for at least 25 years. In another experiment, the preference of *C. maenas* between *N. lapillus*, high spire *L. obtusata* and low spire *L. obtusata* was investigated.

The predation on *L. obtusata* was significantly higher in the treatments with *N. lapillus* from Pembroke than in those with *N. lapillus* from Little Harbor, in both times the experiment was performed. Small *C. maenas* were just able to prey on *L. obtusata* with high spires. Large crabs were able to prey on all three food items, and high spire *L. obtusata* were successfully attacked most often.

GENERAL INTRODUCTION

A predator has to make decisions about what, where and when to eat (Krebs, 1977; Crawley & Krebs, 1992). According to optimal foraging theory, the feeding strategies presented by an organism are designed by natural selection to maximize its net rate of food intake (Krebs, 1977; Hughes, 1980; Crawley & Krebs, 1992).

Predators are expected to select prey items based on their food value. Food value of a prey item depends on its nutritional content, its pattern of spacing and abundance, and the cost of capture and processing (Morse, 1980; Krebs, 1977). The prey food value will also be influenced by the levels on which it exposes the predator to competition with other consumers, and to predation (Morse, 1980).

The food value of different food items may be compared by measuring their size, handling time (the time that a predator takes catching, subduing, consuming, and digesting a prey (Barnes, *et al.* 1993) and / or caloric content. However, these indirect measures may not reflect accurately their value to the consumer in terms of growth or reproduction because they may vary in the total potentially usable energy, and / or processing costs (Palmer, 1983, 1984). Short-term growth rate is, on the other hand, a more

biologically significant measure of net food value to a consumer, because it provides a direct measure of the energy remaining after all costs associated with consuming a prey have been paid (Conover & Lalli, 1974). Growth rate can also be related directly to various fitness attributes such as age or size at first reproduction and total reproductive output, and it has been used to assess food quality for a variety of marine organisms (review in Palmer, 1983).

Besides the decisions about the type of prey, the predator is also confronted with decisions related to the number of prey to be eaten. The feeding rate of an organism will be basically the result of the energetic demands of its metabolism, although other factors may also have an influence such as, prey abundance, predation risk, and environmental factors such as, temperature, wave action, etc. (Edwards & Huebner, 1977; Palmer, 1990; Etter, 1989)

Feeding strategies may also differ with relation to the number of prey items eaten. Dietary generalists eat wider ranges of prey than dietary specialists (Curio, 1976). Specialization should be effective enough to achieve optimal hunting success but at the same time, it should not be so rigid as to prevent the predator from changing from a particular and originally preferred prey species when that species becomes rare (Curio, 1976).

One aspect of the behavior of predators influencing the

range of prey taken is whether predators forage singly or in groups. Where predators forage singly, the average diet may be very wide because different individuals feed on different things or on different proportions of the available prey. Where predators forage in groups, they may tend to have narrower ranges of diet because each individual in the group eats whatever the group finds. Alternatively, the groups may encounter, and feed on, a wider variety of prey, because the group may be attracted to any item that attracts any individual member of the group. This has been proposed as the reason why some predatory whelks form large aggregations while foraging (Jenner, 1958; Crisp, 1969 in Underwood & Fairweather, 1992). Switching of prey items may be common in social animals that feed in flocks (Murdoch & Oaten, 1975 in Underwood & Fairweather, 1992).

When a predator feeds on more than one prey item, it may have a fixed preference for a particular species of prey over the others, and this preference may not change as the density of the available prey changes. In other cases, preference for one prey type depends on the density of prey types available, and the predator switches from one prey type to another (Krebs, 1985). Examples are the predatory gastropods *Thais emarginata* and *Acanthina spirata* that prefer to eat mussels when barnacles comprise less than 75 percent of the available prey, but prefer barnacles when they reach

80 percent or more of the available food items (Murdoch, 1969).

Wood (1968) confirmed that the statistical preference for barnacles by *Urosalpinx cinerea* is not genetically fixed, and studies in the field indicate that ecological factors can account for prey selection in intertidal habitats. However, some components of a diet may be obligatory, and if a predator must include certain items of prey in its diet, then its behavior is likely to include long term persistence in searching for that type of prey, regardless of the availability and relative abundance of other types (Underwood & Fairweather, 1992).

The capacity of a predator to change its diet in response to changes in prey abundance can have a great adaptive value. Switching prey, seems to occur most often between prey which are nearly equally preferred (Krebs, 1985). Prey switching can be important for predators that feed on several types of prey because it could stabilize the density fluctuations of the prey species. As one prey species increases in abundance relative to others, the predator would concentrate their feeding on the numerous prey species and possibly restrict that prey's population growth. On the other hand, switching to alternative foods may help the prey population to recover if it falls to low levels. Switching behavior could thus benefit the predator by maintaining stable prey population sizes (Krebs, 1985).

Nucella lapillus is a slow moving, foraging predator in the intertidal zone. It preys mainly on the mussel *Mytilus edulis*, and on the barnacle *Semibalanus balanoides* (Annala, 1974; Menge, 1976; Crothers, 1977), but predation on the snail *Littorina obtusata* has also been registered (Colton, 1916; Moore, 1938; Lull, 1979). *N.lapillus* has intracapsular metamorphic development (no free larval stage) with newborns hatching out of an egg capsule as juvenile snails (Fretter & Graham,1994). *N.lapillus* also has very limited movement. According to Connell (1961), the average movement of *N.lapillus* during one tidal cycle is 100 mm, and Castle & Emery (1981) stated that the adults of *N.lapillus* do not move more than 30 m in a lifetime. As a consequence, each local population is isolated and there is little, or no interchange of genes between them (Fretter & Graham, 1994).

Mytilus edulis is a very widely distributed bivalve that has been carried from Europe all over the northern hemisphere attached to the bottoms of ships (Yonge & Thompson, 1976). Members of the family Mytilidae are dominant space occupiers, occurring most at exposed or semi-exposed sites in temperate habitats, especially on horizontal or gently sloping rocky substrata (Suchanek,1986). The development of byssal attachment threads by adult bivalves, as in the genus *Mytilus*, has allowed them to exploit hard substrata and dominate rocky habitats (Suchanek, 1986).

Mytilus edulis larvae settle and metamorphose and then move upward before attaching semi-permanently in some depression or between adult mussels; if detached they again become motile before new threads are planted (Yonge & Thompson, 1976). Associated with the evolution of the byssal apparatus is a typical reduction of the anterior end of the body and enlargement of the posterior region, producing a triangular shape and heteromyarian condition (the 'typical' mussel form) (Suchanek, 1986). Secured by byssus threads planted by the elongate foot, the animal can align itself to the forces of the sea while the raised hind end allows ample entrance for an inflowing current created by gills (Yonge & Thompson, 1976). The predator *N.lapillus* is sometimes trapped by the byssus threads of *M.edulis* and held until death (Moore, 1938; Petraitis, 1987).

Littorina obtusata is an intertidal herbivorous prosobranch that lays egg masses attached to a substratum from which newborns hatch, as juveniles snails. As in *N.lapillus*, no free larval stage is found (Fish & Sharp, 1986; Hughes, 1986; Fretter & Graham, 1994).

The green crab *Carcinus maenas*, originally from Europe, was introduced in North America by the end of the last century (Scattergood, 1952; Glude, 1955; Vermeij, 1978, 1982-b; Bliss, 1982)). By 1954, *C. maenas* had been able to extend its range northeastward to Wedgeport, Nova Scotia (Glude, 1955; Taylor,

Bigelow & Graham, 1957; Ropes, 1968). Although a decline in sea surface temperatures after 1957 had sharply reduced populations of *C. maenas* in some areas such as the Bay of Fundy (Welch, 1968), the green crab seems to be a well established species in most of the Atlantic Northeast, and it is considered a very important predator on mollusks. *Carcinus maenas* is probably the most common shore crab of New England at least as far north as the Bay of Fundy (Gosner, 1978). *C. maenas* is found under stones in intertidal and subtidal areas at shallow depths (Gosner, 1978).

The present dissertation investigated several aspects of the interactions between *Nucella lapillus*, *Mytilus edulis*, *Littorina obtusata* and *Carcinus maenas*.

Chapter one investigates the influence of the exposition to a single prey in the development of prey preference by *N. lapillus* and the influence of prey availability on prey recognition capability by *N. lapillus*. The results showed that the maintenance of *N. lapillus* on a single diet reinforces an existing preference for this prey (ingestive conditioning), but does not increase a preference for this prey. Also, my studies indicates that the ability of *N. lapillus* to recognize a new kind of prey, depends on a learning process, which may be trigger by the scarcity in abundance of the preferred prey, *Mytilus edulis*.

Chapter two compares the feeding rate and growth rate

of *Nucella lapillus* preying on *Littorina obtusata* and *Mytilus edulis*. The results demonstrated that *N. lapillus* increases its feeding rate in higher prey density, and that growth rate of *N. lapillus* was higher on a diet of *M. edulis* than on a diet of *L. obtusata*.

Chapter three addresses the influence of predation by *Carcinus maenas* on the predatory behavior of *Nucella lapillus*, and the preference of *C. maenas* between *N. lapillus*, *Littorina obtusata* with a low spire and *L. obtusata* with a high spire. The results indicate that *N. lapillus* predation on *L. obtusata* was not inhibited by the presence of *C. maenas*, and that *C. maenas* prefers high spire *L. obtusata* over low spire *L. obtusata* and *N. lapillus*.

The monitoring of the Pembroke population would be a good test case to observe if the increase in the green crab *Carcinus maenas* density will be followed by changes in the *L. obtusata* and *N. lapillus* morphology.

CHAPTER I

PREY PREFERENCE AND RECOGNITION BY *Nucella lapillus* (LINNAEUS,1758)

Introduction

Predator-prey relationships are of great importance in the control of both predator and prey populations. Predation may prevent a prey population from depleting its food resources. On the other hand, the capacity to change diet when a prey population density decreases below certain levels, may represent a mechanism for preservation of the most favorable food resource by that predator population.

In a harsh environment with a low prey density, search time is long. Therefore, pursuit time for nearly all items encountered is irrelevant in terms of decision making, and the animal has to become a generalist. On the other hand, in a productive environment with short search times, specialization is favored (Curio,1976). MacArthur (1972), using his optimal foraging model, was able to predict that a species should become more specialized in a productive environment in comparison to a harsh one. Nevertheless, specialization should be effective enough to achieve

optimal predation success, but at the same time, it should not be too rigid to prevent the predator from changing from a particular and originally preferred prey species when that species becomes rare (Curio, 1976).

When a predator feeds on more than one prey species, it may have a fixed preference for one species of prey over the others, and this preference may not change as the density of the available prey changes. In other cases, preference for one prey type depends on the relative density of prey types available, and the predator switches from one prey to another (Krebs, 1985, Hassell, 1978).

Some animals increase their preference during prolonged exposure to a particular prey involving a conditioning process called ingestive conditioning (Hughes, 1986) in addition to the more immediate effects of learning. Ingestive conditioning could delay the response of predators to changes in the abundance of prey. A severe delay in this response may cause the local extinction of a prey before preference for it has been lost (Hughes, 1986).

The neogastropod *Nucella lapillus* is a slow moving foraging predator in the intertidal zone, that preys mainly on the mussel *Mytilus edulis*, and on the barnacle *Semibalanus balanoides* (Moore, 1938; Annala, 1974; Menge, 1976; Crothers, 1977; Burrows & Hughes, 1991), which often occur in patches on the shore. *Nucella lapillus* has intracapsular metamorphic development (no free larval

stage) with newborns hatching out of an egg capsule as juvenile snails (Fretter & Graham,1994). *N.lapillus* also has very limited movement. According to Connell (1961), the average movement of *N.lapillus* during one tidal cycle is one 100 mm, and Castle & Emery (1981) stated that the adults of *N.lapillus* do not move more than 30 m in a lifetime. As a consequence, each local population is isolated and there is little, or no interchange of genes between them (Fretter & Granham, 1994).

In the present study, prey preference and recognition of 13 populations of *Nucella lapillus* were investigated: one population from Massachusetts; three from New Hampshire and nine from Maine, U.S.A (Figure1.1). In one beach on the Maine coast, a population of *N.lapillus* was found feeding just on *Littorina obtusata* which usually is not one of the main prey items of *N.lapillus*. Predation on *Littorina obtusata* by *Nucella lapillus* was reported by Colton,1916, Moore,1938, and Lull,1979. The purpose of this study is to test the following hypotheses: (1) *Nucella lapillus* kept on a single prey diet develops a preference for this prey, and (2) prey availability affects prey recognition in this predator.

Study Areas

Study areas are localized in the Gulf of Maine. According to Mathieson, Penniman & Harris (1991) the Gulf of Maine is a partially enclosed sea extending from Nantucket Shoals and Cape Cod, Massachusetts, on the west (70°W , 42°N) to Cape Sable, Nova Scotia, on the east (65°W 43.5°N). The geology of most strata is a complex association of igneous metamorphic rocks that is of late Precambrian and Paleozoic ages (Mathieson, Penniman & Harris,1991).

The study sites were located at Halibut Park, Cape Ann, Massachusetts Hilton Park, Jaffrey Point, Little Harbor, New Hampshire; Boothbay Harbor, two populations from Pembroke separated by about one 100 m from each other, that showed different behavior, one preying on *Littorina obtusata* (Pembroke / LO), and the other preying on *Mytilus edulis* (Pembroke / ME), Reversing Falls, Rockland, Schoodic Point, Spruce Head, West Quoddy Head, and Winter Harbor, Maine (Figure1.1, Table1.1). The degree of exposure to wave action varied between these sites. Exposure indices (EI) based on the classification proposed by Ballantine (1961) are given for each site (Table1.1).

Materials and Methods

Two different experiments were performed: one to test the preference by *Nucella lapillus* between *L. obtusata* and *M. edulis*, and the other to study prey recognition by *N. lapillus*. The first experiment was performed using four populations (Jaffrey Point, Little Harbor, Pembroke / LO and Pembroke / ME) and the second one using all 13 populations.

Preference Experiment

Individuals of *Nucella lapillus* from one population that prey on *Littorina obtusata* (*N. lapillus* / LO) and from three populations that prey on *Mytilus edulis* (*N. lapillus* / ME) in the field, were placed separately in 13X13X10 cm plastic boxes. Each *N. lapillus* was placed with five *Mytilus edulis* (10-30 mm) and five *Littorina obtusata* (10-12 mm). For controls, individuals from the population of *N. lapillus* / LO were placed separately in plastic boxes with ten *L. obtusata* each, and individuals from the populations that prey on *M. edulis* were placed separately in plastic boxes with ten *M. edulis* each.

During the experiment the number of consumed prey was noted and eaten individuals were replaced. This experiment lasted for one month at 15°C and was replicated ten times for the adults of

the four populations studied. The mean number of individuals of *Littorina obtusata* and *Mytilus edulis* consumed was calculated for each *N. lapillus* population. The experiment was repeated with juveniles of the four populations in five replicates.

Recognition Experiment

Individuals of *Nucella lapillus* from the population that prey on *Littorina obtusata* (*N. lapillus* / LO) were placed in plastic boxes with *Mytilus edulis*. *N. lapillus* from 12 other populations that feed on *M. edulis*, were placed in plastic boxes with *L. obtusata*. Ten boxes were utilized for each population. Each box had one predator and five prey. For controls, individuals from the population of *N. lapillus* / LO were placed separately in plastic boxes with five *L. obtusata* each, and individuals from the other 12 populations were placed separately in plastic boxes with five *M. edulis* each. The percentage of individuals that were able to prey on the new items, and the amount of time they took to perform this diet change was noted. These experiments were done at a temperature of 8°C for four populations and at 15°C for all 13 populations.

The West Quoddy Head site is a very heterogeneous area so the experiments in recognition with this population were repeated twice. The first experiment was done with individuals of

N. lapillus collected randomly from the shore. In the second experiment individuals of *N. lapillus* from areas that had just barnacles were tested separately from individuals from mussel sites and from periwinkle sites.

Other Observations

The handling time of the predation on *Littorina obtusata* and *Mytilus edulis* by *Nucella lapillus* was measured by placing one adult predator with one prey into separate containers. These experiments were replicated ten times for each prey. Observations were made every six hours over a 30 day period. The time interval from the first successful attack to the separation of the empty shell from the predator was recorded.

The caloric content of the tissues of each prey was determined (method ASTM D240, Midwest Laboratories) and used to calculate the energy obtained per prey consumed. These results were then used to compare the relative caloric value of each prey type.

To measure the prey availability in these sites, 0.10m² quadrats were arranged along transects. The number of *L. obtusata* and *M. edulis* present, the number of *N. lapillus* that were feeding, the type and size of the prey, and any other predator activities (resting, mating, etc.) were counted for each quadrat. Analysis of

variance (ANOVA), regression and the chi-square test were used to compare the different sets of data collected.

Results

Preference

Both adult and juvenile individuals of *Nucella lapillus* from all four populations showed a preference for *Mytilus edulis*, during the 1 month experiment, consuming a greater number of this prey than of *Littorina obtusata* (Figures 1.2 and 1.3). Individuals from the population of Jaffrey Pt., New Castle, NH did not prey on *Littorina obtusata* consuming exclusively *Mytilus edulis* during this experiment (Figures 1.2 and 1.3). The difference in the numbers of prey eaten among all populations was statistically significant ($\alpha < 0.001$).

Recognition

All 13 populations studied were able to recognize *Littorina obtusata* as prey except the population from Jaffrey Pt., New Castle, NH (Figures 1.4 and 1.5). In the other three populations (Little Harbor, NH; Pembroke / LO, Pembroke / ME) where the experiments were performed at two different temperatures the recognition was faster and / or involved more individuals at 15°C than at 8°C (Figure 1.5). The difference in the number of individuals

that recognized prey among populations was statistically significant ($\alpha < .025$ at 8°C and $\alpha < .001$ at 15°C).

The percentage of individuals of *N. lapillus* that were able to recognize *L. obtusata* as prey was significantly higher in the populations from sheltered areas than in the populations from exposed areas ($p < .001$) (Figure 1.6). Among the seven sheltered beaches the percentage of recognition of *L. obtusata* as food by individuals of *N. lapillus* was highest in Boothbay Harbor, where the more abundant prey was *Semibalanus balanoides* (Figure 1.6). Among the five exposed beaches the percentage of recognition of *L. obtusata* as prey by individuals of *N. lapillus* was highest for Halibut Park, where the more abundant prey was *Mytilus edulis* (Figure 1.6) though most individuals, were very small, probably due to the high wave action. Some individuals of *N. lapillus* from the population at Halibut Park were observed successfully preying on *L. obtusata* by the aperture instead of drilling through the shell. The percentage of *N. lapillus* recognition on *L. obtusata* was not significantly related to the abundance of *L. obtusata* or *M. edulis* in the field in the 12 studied populations (Figure 1.7).

The percentage of recognition of *L. obtusata* by *N. lapillus* in West Quoddy Head presented a significant variation among the different collecting sites. The individuals collected randomly on the

shore showed 20% recognition, but those collected in the mussels, barnacles and periwinkle sites presented respectively 40, 30, and 60 % of recognition. These results showed that individuals from areas with more *L. obtusata* had a higher capacity to recognize this species as prey, probably by having prior experience with this prey.

Mytilus edulis was significantly more abundant in exposed areas than in sheltered areas ($p < .017$). On the other hand there was no significant difference in the abundance of both *Littorina obtusata* and *Semibalanus balanoides* between sheltered and exposed areas (Figure 1.8). Although sheltered areas showed a higher percentage of recognition for *L. obtusata* and lower abundance on *M. edulis* than exposed areas, these two variables were not significantly correlated.

The handling time was longer when *N. lapillus* preyed on *L. obtusata* (67.8 h, ± 3.25 SE, range 12-190, N=86) than when it preyed on *M. edulis* (52.7 h, ± 3.25 SE, range 12-174, N=84) (Figure 1.9 and Table 1.2). The caloric content found in *L. obtusata* was 4.330 cal/g and in *M. edulis* was 3.536 cal/g. However as *M. edulis* are larger (10 - 25 mm in length) than *L. obtusata* (10 - 12 mm in length) the caloric content per individual was higher for the former (1.63 cal.) than for the latter (0.48 cal.) (Table 1.3).

Discussion

The preference for *Mytilus edulis* over *Littorina obtusata*, demonstrated in the present study by the individuals of all four populations of *Nucella lapillus*, may be due to the fact that *M. edulis* is a more energetically lucrative prey. Individuals of *M. edulis* require a shorter handling time and have a higher caloric content per individual than *L. obtusata*. Hughes (1986), based on his observations that *N. lapillus* increases its preference during prolonged exposure to a particular prey, concluded that *N. lapillus* shows ingestive conditioning.

According to Wood (1968), ingestive conditioning is a modification and/or reinforcement of prey preferences in response to chemicals from prey that had been consumed recently. Ingestive conditioning may involve a training process (Hall, et al., 1982). In birds, this training involves the formation of a search image (Royama, 1970; Dawkins, 1971). In gastropods the process was shown after the predator had many encounters with the prey (Murdoch, 1969) but it must be chemical and not visual as in birds.

In the present study, *Nucella lapillus* from Pembroke / LO had probably only eaten *L. obtusata* in the field (no mussels and barnacles were found in this site), recognized *Mytilus edulis* as food within the first week of the experiment. They preferred it over *L. obtusata*, suggesting that *N. lapillus* does not show ingestive

conditioning (Figure 6). On the other hand, the failure of the Jaffrey Point population to recognize *L. obtusata* may have been a result of the ingestive conditioning process: the very low abundance of *L. obtusata* in this area could have reinforced the preference by *N. lapillus* for the more lucrative prey.

These data suggest that predator experience would lead to ingestive conditioning when the food item is the one already preferred by the predator, but not when it is an item not usually important in the diet. Murdoch (1969) studied preference, training and switching in *Thais emarginata* and *Acanthina spirata*, and found that when the preference was strong the predators did not switch, but when the preference was weak the predators were easily trained and switched.

The production of bore holes in unusual places, by *Nucella lapillus* from Jaffrey Point newly exposed to *L. obtusata* as a prey, seems to be an indication of a lack of prior experience with this prey. According to Hughes & Dunkin (1984), when *N. lapillus* that had eaten only barnacles, began to drill on *M. edulis*, it drilled the hole in random positions on the mussel shell; but after consuming some *M. edulis*, the snails developed a tendency to drill in the thinnest area of the mussel shell up to 25 mm in length. They drilled over the digestive gland in larger mussels. Moreover, Morgan (1972) showed that *N. lapillus* reduced the handling time when preying on *M. edulis*

after accumulating experience with this prey.

When *L. obtusata* was offered without a shell to the individuals of *N. lapillus* from the Jaffrey Point population, some of them ate the prey. After that, these individuals started recognizing *L. obtusata* as prey. However, they initially did not drill the prey in the place usually chosen by *N. lapillus* : the dorsal side between the spire and the body whorl (Lull,1979). Instead, these animals drilled the bore hole in different sites on the body whorl. Nevertheless, after they had eaten several prey, they started drilling between the spire and the body whorl, where it is over the visceral mass, similar to experienced *N. lapillus* from other locations.

It seems that *N. lapillus* has the capacity to prey on *L. obtusata* but requires some experience to learn how to do it. The recognition of *L. obtusata* as a prey by *N. lapillus* from the other eleven populations studied, may be a consequence of previous experience with this prey in the field.

The fact that individuals from Halibut Park showed a much higher percentage of recognition of *L. obtusata* as prey than at other exposed areas is probably related to the relatively small size presented by *M. edulis* in this area. This would enhance the value of *L. obtusata* as a prey in comparison to *M. edulis*, since the former presents a higher caloric content per gram than the latter.

The absence of *M. edulis* and *S. balanoides* in Pembroke /LO area may be due to the scarcity in this area of *L. littorea*. Petraitis (1983), Bertness (1984) and Bertness et al. (1983) showed evidence that grazing by *Littorina littorea* in New England may enhance barnacle settlement and even lead to the replacement of salt marsh habitats by rocky ones (Bertness, 1984). Other factors that may limit the settlement of barnacle and mussels are the muddy substrate, a limited planktonic larval supply, adverse water column factors or space limitation on the shore (Connell, 1985).

The small abundance of *M. edulis* in the sheltered areas is probably the reason why the *N. lapillus* from these areas were more able to recognize *L. obtusata* as a prey than the individuals from the exposed areas where *M. edulis* is more abundant. Menge (1976,1978,1983) showed that food availability is greater at exposed shores and decreases as shores become more sheltered. The scarcity of its preferred prey probably led the individuals of *N. lapillus* in the sheltered areas to prey occasionally on *L. obtusata*. The ability to recognize this prey in the experiment, would be a consequence of previous experience with *L. obtusata* in the field. The ability to recognize *L. obtusata* by the twelve populations studied may be due also to chance encounters in the field. West (1988) studied a population of *Thais melones* and found in the same population some individuals were specialists and others were

generalists. According to West (1988) this difference between individuals, based on the fact that each individual increased its efficiency by repeatedly handling the same type of prey, because this reduced the time taken to identify, attack and consume the prey. This probably explains how individuals eventually get their particular feeding preferences, and probably also explains how and why predators start to switch to relatively more abundant prey (Murdoch, 1969).

Conclusion

The maintenance of *Nucella lapillus* on a single diet, reinforced an existing preference for this prey (ingestive conditioning), but did not form a preference for this prey. The ability of *N. lapillus* to recognize a new kind of prey, depends on a learning process (ingestive conditioning), which is triggered by the scarcity in abundance of the preferred prey *Mytilus edulis*.

Table 1.1. Summary of 13 study sites, locations, coordinates, and exposure indices based on Ballantine (1961).

LOCATION	COORDINATES	EXPOSURE INDICES (EI) BASED ON BALLANTINE (1961)	CHARACTERISTICS
Halibut Park, Cape Ann, Ma	42°41'N, 70°38'W	extremely exposed (EI=1)	<i>M.edulis</i> is common in the lower mid littoral as very tiny, crowded individuals, and <i>N.lapillus</i> has a short spire and large aperture
Hilton Park, NH	43°07'N, 70°50'W	fairly sheltered (EI=5)	<i>S.balanoides</i> and <i>N.lapillus</i> are common in the mid littoral
Jaffrey Point, NH	43°03'N, 70°43'W	semi-exposed (EI=4)	the dominant algae are <i>Fucus sp.</i> and <i>Ascophyllum sp.</i> and the dominant animals are <i>S.balanoides</i> (Annala, 1974; Mathieson et al, 1981) and <i>N.lapillus</i> are common on the open rock
Little Harbor, NH	43°03'N, 70°43'W	sheltered (EI=6)	<i>S.balanoides</i> , <i>L.obtusata</i> and <i>N.lapillus</i> are common in the mid littoral
Boothbay Harbor, NH	43°51'N, 69°38'W	fairly sheltered (EI=5)	<i>S.balanoides</i> and <i>N.lapillus</i> are common and <i>L.obtusata</i> is frequent on the furoids in the mid littoral
Pembroke/LO, Me	44°52'N, 67°13'W	very sheltered (EI=7)	<i>L.obtusata</i> is abundant on <i>Ascophyllum sp.</i> that covers most of the mid littoral, and <i>N.lapillus</i> has a long shell
Pembroke/ME, Me	44°52'N, 67°13'W	very sheltered (EI=7)	<i>M.edulis</i> is common as groups of large specimens, <i>L.obtusata</i> is abundant and <i>N.lapillus</i> has a long shell
Reversing Falls, Me	44°52'N, 67°13'W	exposed (EI=3)	<i>M.edulis</i> is abundant and <i>N.lapillus</i> is common
Rockland, Me	44°06'N, 69°06'W	fairly sheltered (EI=5)	<i>S.balanoides</i> , <i>L.obtusata</i> and <i>N.lapillus</i> are common
Schoodic Point, Me	44°20'N, 68°05'W	very exposed (EI=2)	<i>S.balanoides</i> , <i>M.edulis</i> are common and <i>N.lapillus</i> has a short spire and large aperture
Spruce Head, Me	44°00'N, 69°07'W	very sheltered (EI=7)	<i>S.balanoides</i> , <i>M.edulis</i> , and <i>L.obtusata</i> are common, and <i>N.lapillus</i> has a long shell
West Quoddy Head, Me	44°49'N, 69°59'W	semi-exposed (EI=4)	<i>S.balanoides</i> and <i>N.lapillus</i> are common
Winter Harbor, Me	44°20'N, 68°05'W	sheltered (EI=6)	<i>S.balanoides</i> and <i>N.lapillus</i> are common in the mid littoral

Table 1.2. Handling time of predation by *Nucella lapillus* on *Littorina obtusata* and *Mytilus edulis*

	<i>Mytilus edulis</i>	<i>Littorina obtusata</i>
Number of observations:	120	120
Replicate number:	15	15
Total observations:	1800	1800
Total prey consumed/predator:	7.06	7.13
Number of observations feeding (%):	603 (33.5 %)	808 (44.8 %)
Number of observations not feeding (%):	1197 (66.5 %)	992 (55 %)
Mean handling time per prey (SE):	52.1 (3.25) hours	67.8 (3.25) hours

Table 1.3. Caloric content of *Littorina obtusata* and *Mytilus edulis*

	<i>Littorina obtusata</i>	<i>Mytilus edulis</i>
N:	151	53
Size:	10 - 12 mm	10 - 25 mm
Total wet weight:	17 g	26 g
Calories level found:	4,330 cal/g	3,536 cal/g
Moisture (Convection Oven):	77.5 %	78.2 %
Calories, detection limit, method:	0.01 ASTM D240	0.01 ASTM D240
Moisture, detection limit, method:	0.1 USDA MOI	0.1 USDA MOI
Caloric content / individual:	0.48 cal	1.63 cal

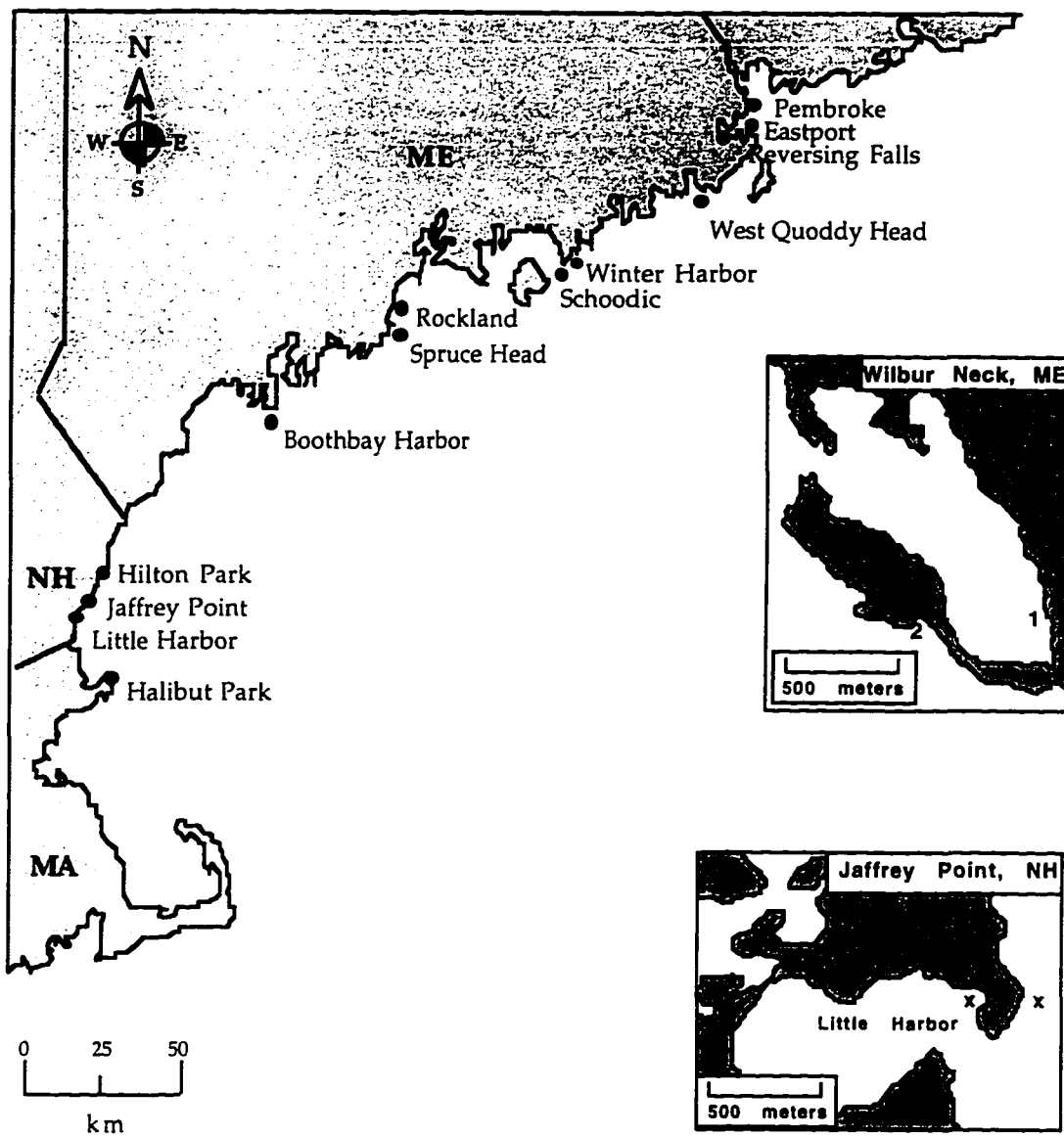


Figure 1.1 Map of Gulf of Maine showing the 13 study areas.
 (1) *Littorina obtusata* site. (2) *Mytilus edulis* site.

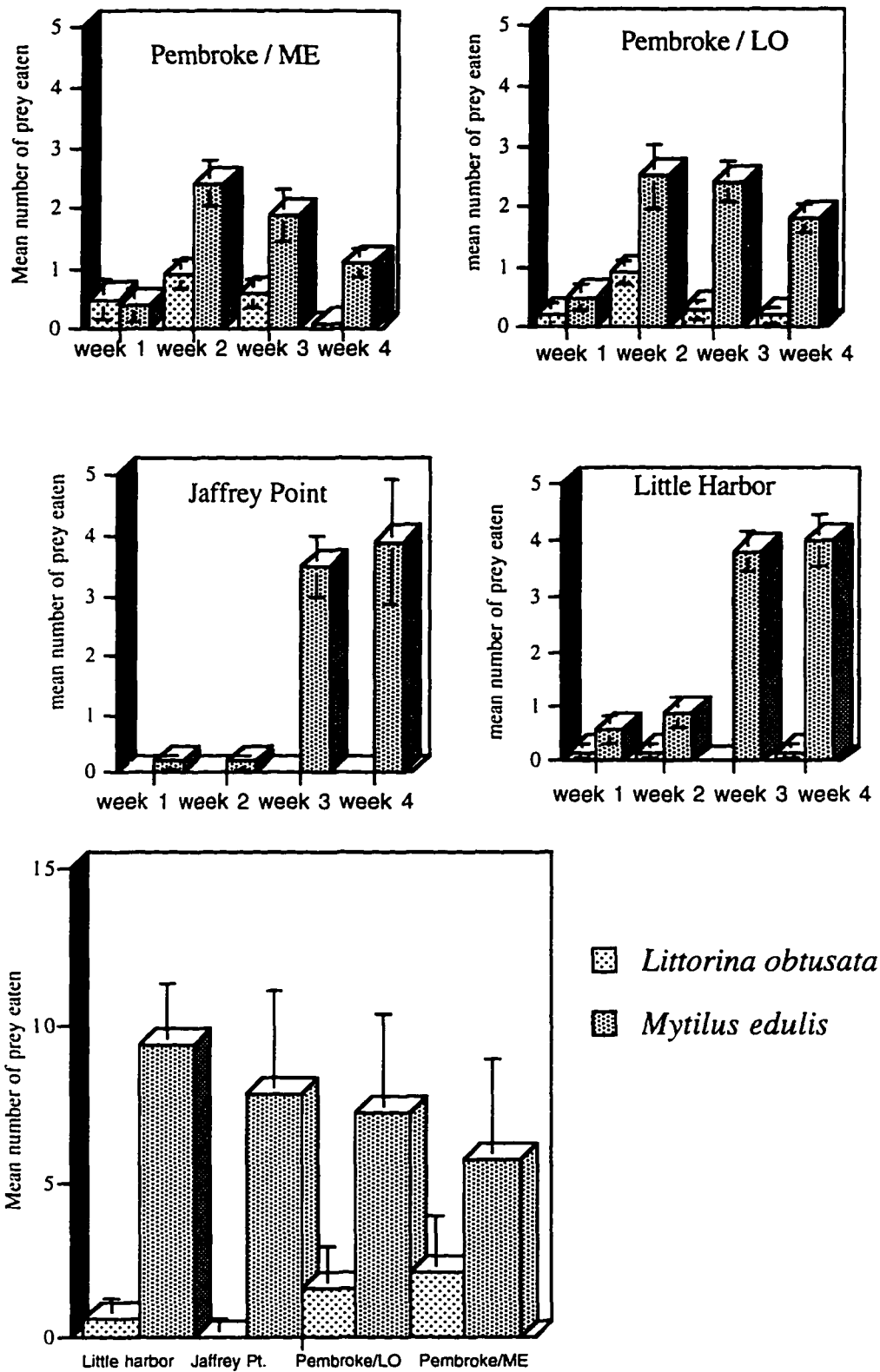


Figure 1.2 Mean number of individuals of *Littorina obtusata* and *Mytilus edulis* eaten by one adult individual of *Nucella lapillus* from four different populations during a 30 day period experiment.

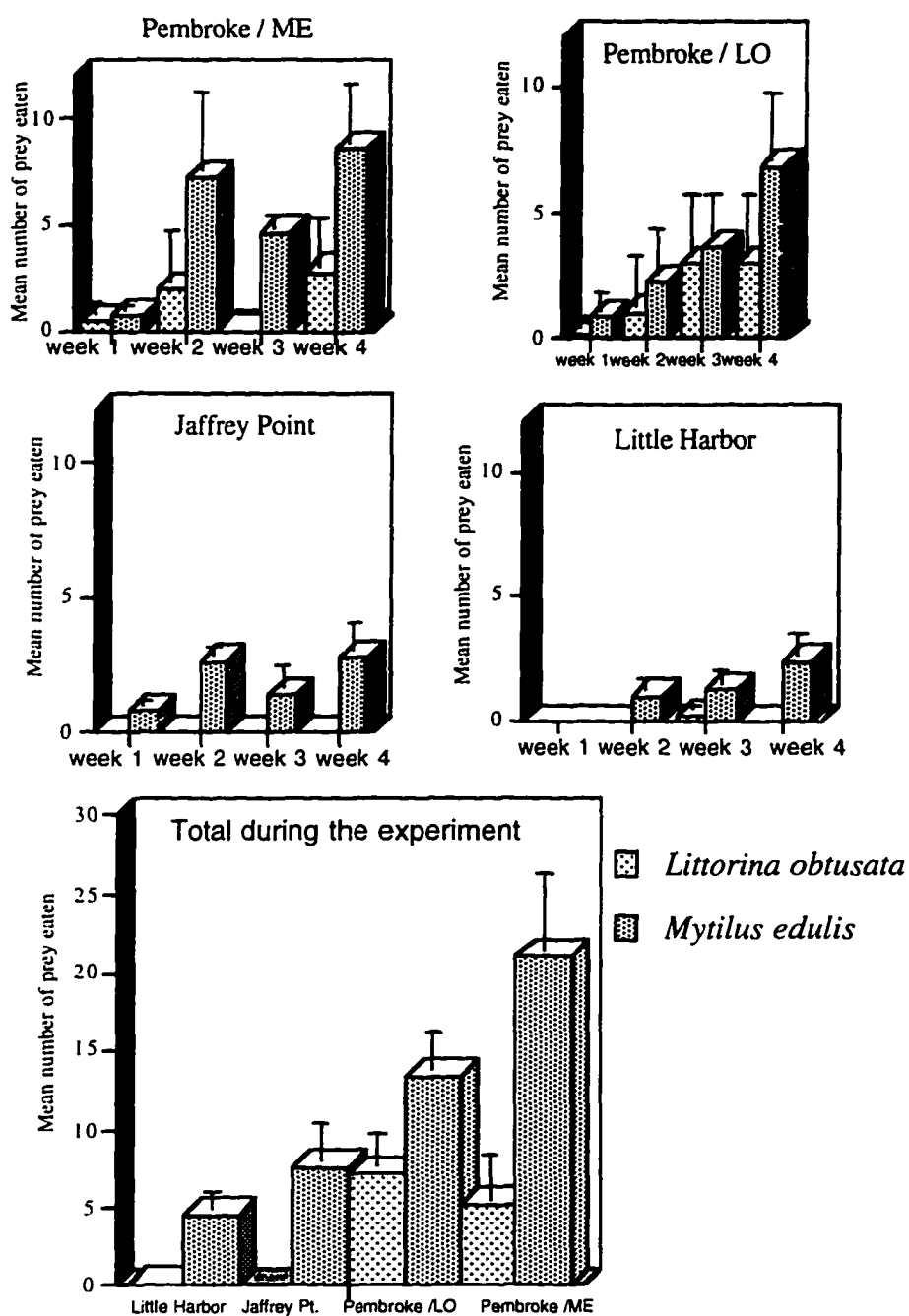


Figure 1.3. Mean number of individuals of *Littorina obtusata* and *Mytilus edulis* eaten by one juvenile individual of *Nucella lapillus* from four different populations during a 30 day period experiment. Error bars = SD.

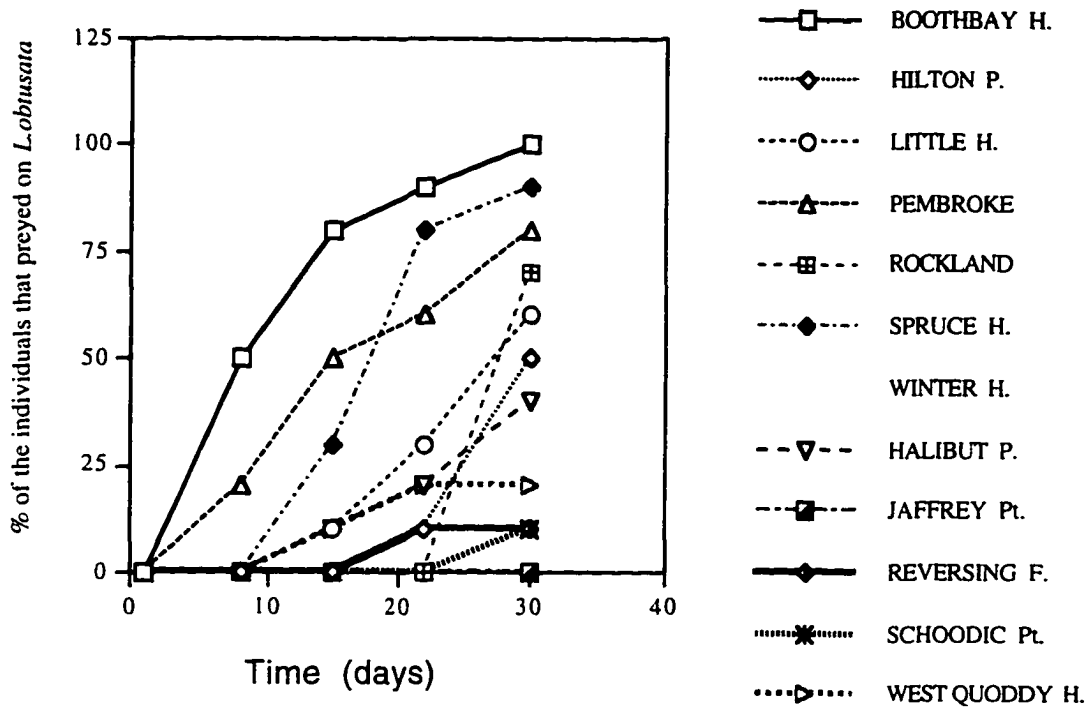


Figure 1.4. Cumulative percentage of individuals (N=10) of *Nucella lapillus* from twelve populations that recognize *Littorina obtusata* as prey during a 30 days period, at a temperature of 15°C

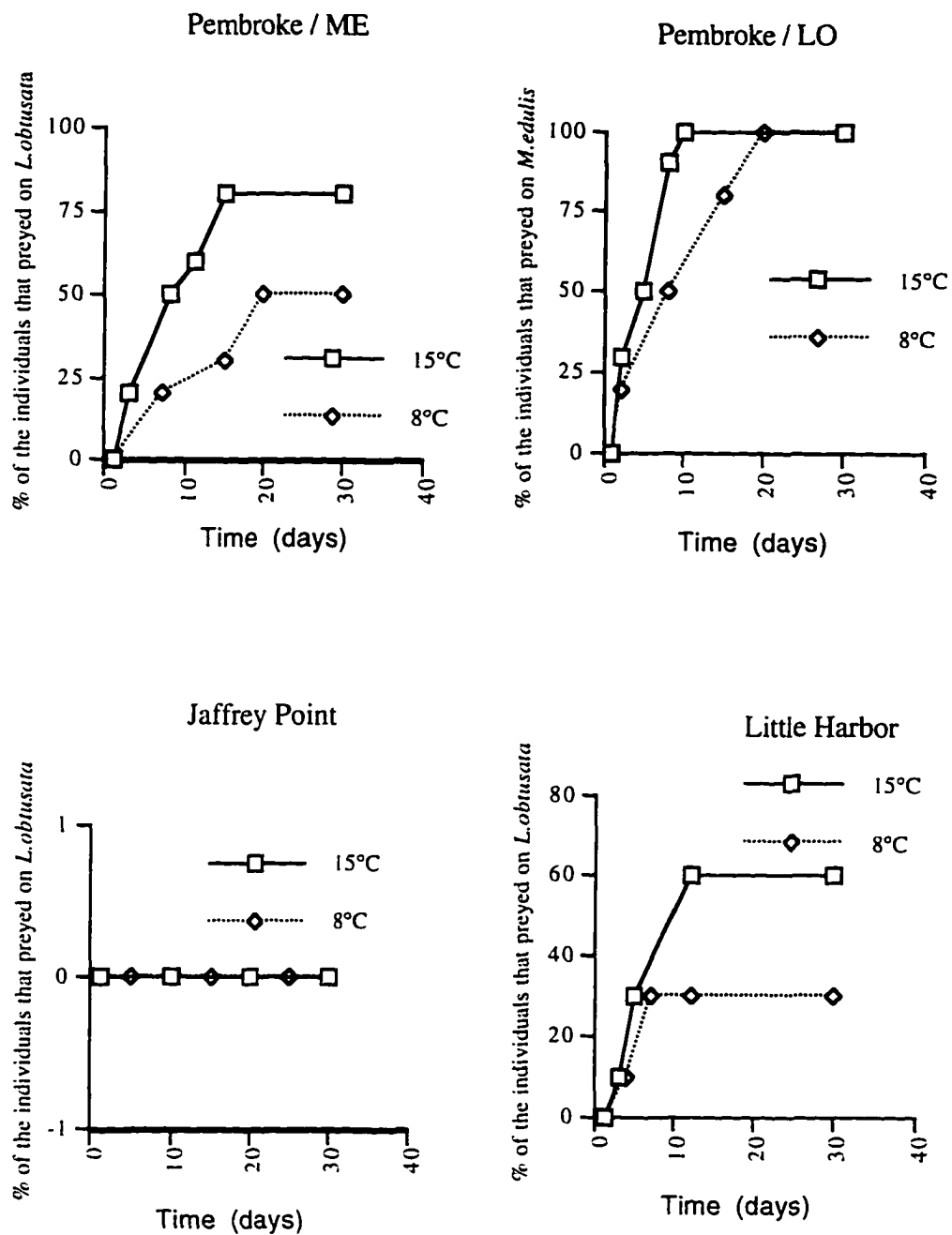
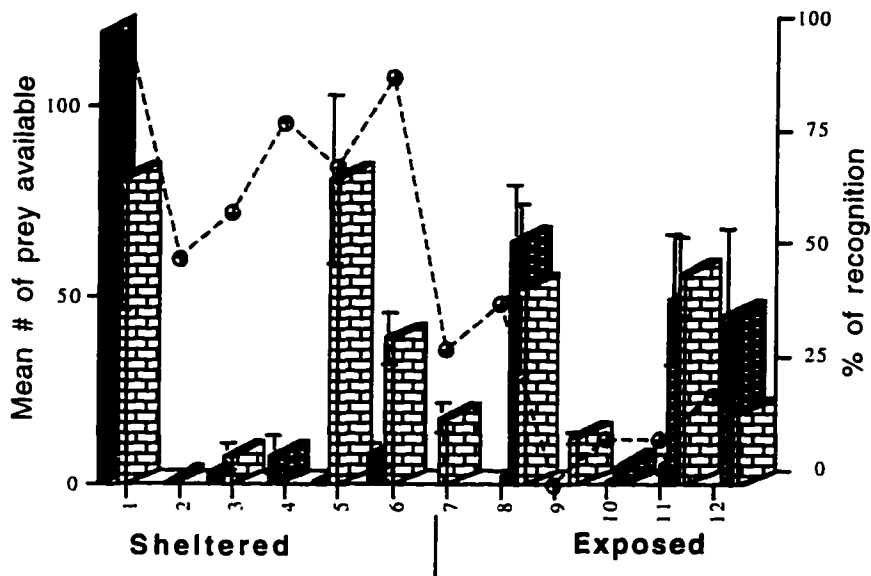


Figure 1.5. Cumulative percentage of individuals of *Nucella lapillus* from four populations that recognize new prey during a 30 day period, at temperature of 8°C and 15°C.



- 1- Boothbay Harbor
- 2- Hilton Park
- 3- Little Harbor
- 4- Pembroke
- 5- Rockland
- 6- Spruce Head
- 7- Winter Harbor
- 8- Halibut Park
- 9- Jaffrey Point
- 10- Reversing Fall
- 11- Schoodic Point
- 12- West Quoddy Head

- L. obtusata
- ▨ M. edulis
- ▩ S. balanoides
- ◆--- % of recognition

Figure 1.6. Mean number of prey available for each *Nucella lapillus* in seven sheltered and five exposed sites during spring, summer and fall, 1994-96 and percentage of *N. lapillus* that recognized *Littorina obtusata* as food. Error bars = SD.

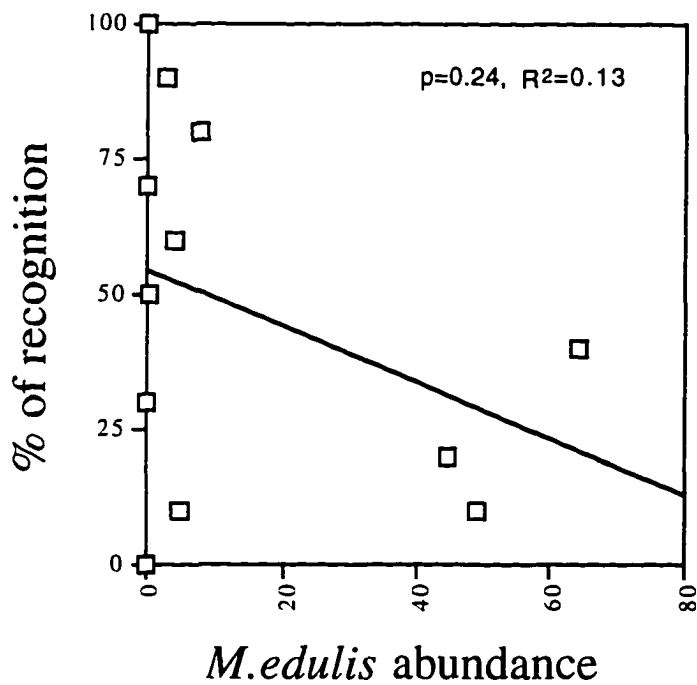
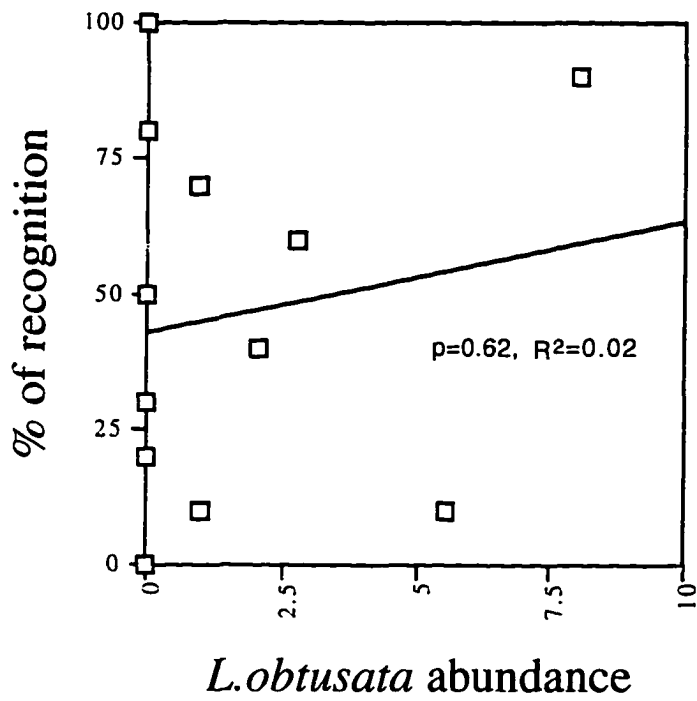


Figure 1.7. Relationship between *Littorina obtusata* and *mytilus edulis* abundance and percentage of *Nucella lapillus* that recognized *Littorina obtusata* as prey in 12 sites.

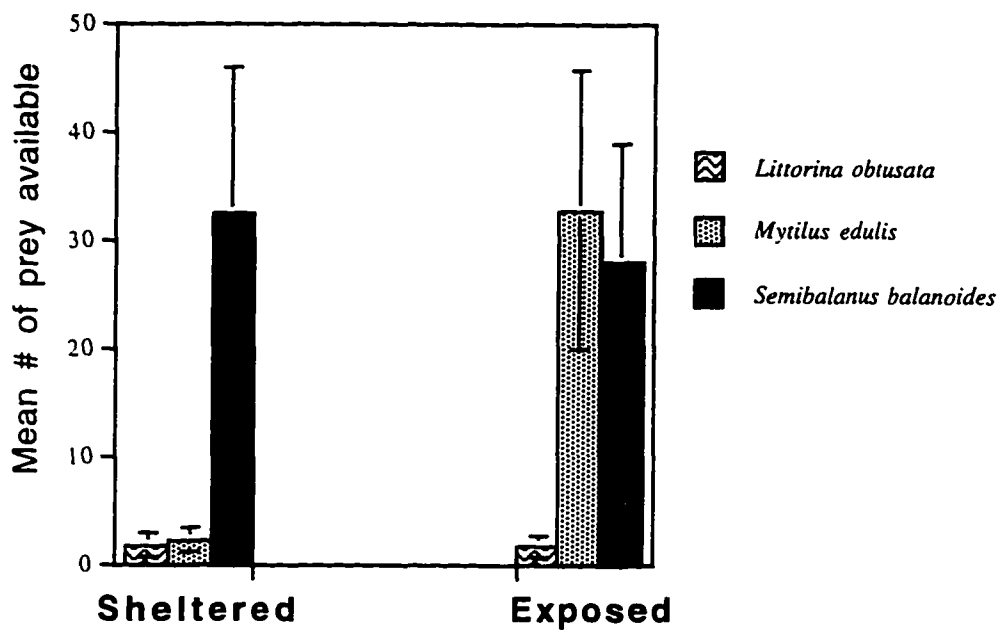


Figure 1.8. Mean number of prey available for each *Nucella lapillus* in all 7 sheltered sites and in all 5 exposed sites. Error bars = SD

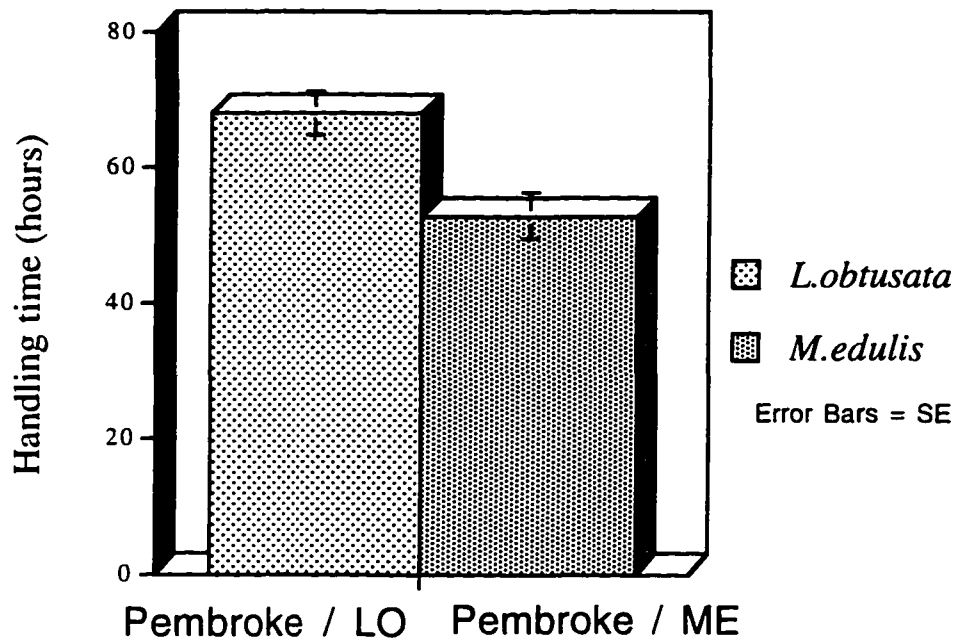


Figure 1.9. Handling time of individuals from the population Pembroke / LO preying on *Littorina obtusata*, and individuals from the population Pembroke / ME preying on *Mytilus edulis*. Error bars = SE.

CHAPTER II

FEEDING RATE AND GROWTH RATE OF *Nucella lapillus* (LINNAEUS, 1758) PREYING ON *Littorina obtusata* (LINNAEUS, 1758) AND *Mytilus edulis* (LINNAEUS, 1758)

Introduction

Predators usually select their food from a variety of potentially available prey items that present different nutritional values, patterns of spacing and abundance, and costs of capture and processing (Hughes, 1980; Morse, 1980; Palmer, 1984; Brown & Richardson, 1987; Burrows & Hughes, 1989, 1991). Moreover, each prey exposes the predator to different levels of competition with

other consumers, and to different levels of predation (Morse, 1980).

Because the animal has only limited amounts of time and energy, its choices among different potential foods may critically affect its survival and reproductive success (Hughes, 1980; Morse, 1980; Palmer, 1984; Brown & Richardson, 1987; Burrows & Hughes, 1989, 1991). Consequently, predators are expected to present a preference for prey with higher "food value" (Hughes, 1980; Palmer, 1984; Brown & Richardson, 1987).

Indirect measures of the value of food items such as size, or caloric content may not reflect accurately their value to the consumer in terms of growth or reproduction because, as stated above, they may vary in the length of time to be consumed, total potentially usable energy, and processing costs (Palmer, 1983, 1984). Short-term growth rate is, on the other hand, a more biologically significant measure of net food value to a consumer, because it provides a direct measure of the energy remaining after all costs associated with consuming a prey have been paid (Conover & Lalli, 1974). Growth rate has yet the additional appeal to be related directly to various fitness attributes as age or size at first reproduction and total reproductive output, and it has been used to assess food quality for a variety of marine organisms (review in Palmer, 1983).

Besides the decisions about the type of prey, the

predator is also confronted with decisions related to the number of prey to be eaten. The feeding rate of an organism will be basically a result of the energetic demands of its metabolism, although other factors may also have an influence, such as prey abundance, predation risk, and environmental factors, such as temperature (Edwards & Huebner, 1977; Palmer, 1990).

The neogastropod *Nucella lapillus* is a slow moving foraging predator in intertidal zone, that preys mainly on the mussel *Mytilus edulis*, and on the barnacle *Semibalanus balanoides* (Annala, 1974; Menge, 1976; Crothers, 1977). *Nucella lapillus* preys also on *Littorina obtusata* (Colton, 1916; Moore, 1938; Lull, 1979).

Previous studies have demonstrated a *N. lapillus* preference for *Mytilus edulis* over *L. obtusata* (Chapter 1). It was also suggested that for *N. lapillus*, *M. edulis* is a more advantageous prey than *L. obtusata*, for presenting a higher caloric content per individual, and requiring a shorter handling time (Chapter 1).

In this study, growth rates of *Nucella lapillus* on diets of *Littorina obtusata* or *Mytilus edulis* were compared. In addition, experiments were conducted to determine whether feeding rates of *N. lapillus* on *M. edulis* and *L. obtusata* were influenced by the abundance of the prey.

Studies Areas

In the present study, four populations of *N.lapillus* were investigated: two from New Hampshire (Jaffrey Point and Little Harbor) and two from Pembroke, Maine. Jaffrey Point is a semi-exposed site (exposure indice= 4 Ballantine, 1961), with *Fucus* sp., *Ascophyllum* sp. and *Semibalanus balanoides* as the dominant organisms (Annala,1974; Mathieson et al,1981,) and *Nucella lapillus* abundant on open rock surfaces. Little Harbor is a sheltered site (exposure indice= 6 Ballantine, 1961) with *Semibalanus balanoides*, *Littorina obtusata*, and *Nucella lapillus* abundant in the mid littoral. Pembroke is a very sheltered site (exposure indice=7 Ballantine, 1961) with two populations of *N.lapillus* separated by about one hundred meters from each other: one feeding on *Mytilus edulis* (no barnacles were found in this site), and the other on *Littorina obtusata* (no barnacles or mussels were found in this site).

Materials and Methods

Adults and juveniles of *N.lapillus* from the Jaffrey Point and Little Harbor populations and adults of *N.lapillus* from both Pembroke populations, were collected and transferred to the laboratory. There, they were kept inside plastic boxes with screen in the sides, in a well aerated aquaria at a constant temperature of 15°C, for two weeks prior to the beginning of the experiment.

Feeding Rate Experiment

In order to test the hypothesis that the feeding rates of *N. lapillus* on *M. edulis* and *L. obtusata*, are influenced by the density of the prey, individuals of all four populations of *N. lapillus* were placed in separate boxes with three or five prey items. Each *N. lapillus* from the Pembroke population that ate *L. obtusata* in the field was placed with three or five *Littorina obtusata* (10-12 mm). Each *N. lapillus* from the other three populations was placed with three or five *Mytilus edulis* (20-30 mm). This experiment lasted for a month and was replicated five times. The average number of prey eaten in each treatment was compared in all four populations. The boxes from each population and each treatment were placed in different aquaria.

Growth Rate Experiment

To determine which one of the diets allows *Nucella lapillus* the higher growth rate, two groups of ten juveniles from Pembroke, that eat *Littorina obtusata* in the field were placed in separate boxes. One group was fed with *Mytilus edulis* (10-30 mm) and the other with *L. obtusata* (5-12 mm), during an 8 month period. The measurements of shell length were made at least once a month and the food consumed were replaced once a week, this way *N. lapillus* always had enough food. The mean number and size of the

prey consumed in each treatment were compared.

Size in Natural Populations

To compare the size of the individuals of both *Nucella lapillus* populations from Pembroke, in June 1994, 0.10 m² quadrats were arranged along transects in both sites, and all *N. lapillus* sampled (87 in the population that eat *L. obtusata* in the field, and 97 in the population that eat *M. edulis*) were measured.

Measurements Proceedings

All shell measurements were made with a vernier caliper to 0.1mm. *M. edulis* shell length was the maximum dimension parallel to the long, ventral margin of the shell. *L. obtusata* shell length was the distance from the apex to the farthest point of the outer lip. The shell length of *N. lapillus* was the distance from the apex to the tip of siphonal canal. Analysis of Variance (ANOVA) was used to compare the different sets of data collected.

Results

Adult individuals of *Nucella lapillus* from all four populations showed higher feeding rates in the treatment with five prey than in the one with three prey (Figures 2.1 and 2.2), although

the difference was statistically significant just in the *N. lapillus* population from Pembroke that prey on *M. edulis* in the field ($p=0.002$). Juvenile individuals of *N. lapillus* from Jaffrey Point and Little Harbor also showed higher feeding rate in the treatment with five *M. edulis* than in the one with three (Figures 2.1 and 2.3). The difference was statistically significant for the Little Harbor population ($p=0.002$).

The decrease in the feeding rate observed during the experiment with adults (Figure 2.2), is probably due to the satiation of the animals after the first few days. Such decrease was not observed among the juveniles, probably because the growth process that they were undergoing demands increasing amounts of food (Figure 2.3).

Nucella lapillus showed a higher growth rate feeding on *Mytilus edulis* than on *Littorina obtusata* ($p<0.001$) (Figure 2.4). The difference in growth rate was already evident two months after the beginning of the experiment (Figure 2.4). The mean number of *M. edulis* eaten per predator (41.6 ± 5.34 , range 33-50, $N=10$) was not significantly different to the number of *L. obtusata* eaten per predator (42 ± 8.60 , range 21-51, $N=10$). On the other hand, the mean size of *M. edulis* eaten by each predator (17.03 ± 1.74 mm, range 14.18-20.05 mm) was significantly higher ($p<0.001$) than the mean size of *L. obtusata* eaten by each predator (8.71 ± 1.21 mm, range

6.63-10.71 mm).

The mean size of the individuals of *N. lapillus* from Pembroke that prey on *M. edulis* on the field ($25.19 \text{ mm} \pm 6.00 \text{ SD}$, range 8-33.1, $N = 97$) was also significantly higher ($p < 0.001$) than the mean size of the individuals of *N. lapillus* that prey on *L. obtusata* on the field (19.91 ± 5.99 , 5-33.1, $N = 87$). Both results above indicate that *M. edulis* has greater "food value" than *L. obtusata*.

Discussion

The positive correlation between feeding rate and prey density, observed in this study, may represent an adaptative response to the increase of the concentration of chemosensory or tactile cues of prey presence as *Nucella lapillus* is a nonvisual predator relying entirely on chemosensory or tactile cues (Kohn, 1961, Hyman, 1967, Hughes, 1986, Fretter & Graham, 1994). On the other hand, such a predator response to an increase in prey abundance may also represent an adaptative response, as an increase in prey abundance can reduce predation costs related to capture, competition, and risk of predation. Juveniles of *Thais haemastoma floridana* also showed an increase in predation rate at higher prey densities (C.Rocha, personal communication).

Predators are designed by natural selection to maximize

the net rate of food intake while foraging (Krebs, 1977; Hughes, 1980; Brown & Richardson, 1987). This optimizing of efficiency by a predator is usually seen in cases of predator choices among prey when foraging. However, the increase in the feeding rate at higher densities of prey could also increase its optimal intake without having to choose among different prey. According to Murdoch (1971), gastropods tend to reach their maximum feeding rate faster as prey density increases because they probably feed until satiated and tend to eat all of an individual prey if possible. This could explain the decrease in the feeding rate in the *N. lapillus* adults after a short period of feeding.

According to the optimal foraging theory, the predator tries to maximize the food intake with less cost, and this could lead to a faster growth (Stephens & Krebs, 1986; Duarte, 1996). In prosobranch mollusks, animal growth is usually estimated by variation in the shell size (Randall, 1964; Frank, 1965; Kenny, 1977; Spight, 1974; Yamaguchi, 1977; Kato, 1989), although, some authors suggest that the best way to estimate growth is by measuring the increase in animal weight (Palmer, 1982).

The formation of the molluscan shell is by the advancing mantle edge, and different shell shapes are formed, by an increased or decreased rate of shell deposition at various points around the circumference of the mantle (Wilbur & Saleuddin, 1983; Laxton,

1970). Body growth and shell growth in most mollusks have to occur simultaneously in order to ensure their correct functional interrelationship (Josse & Geraets, 1983). Consequently, variation in shell size is a good estimate of animal growth in prosobranch mollusks.

According to Burrows & Hughes (1990) *N. lapillus* showed more shell growth on a diet of *Semibalanus balanoides* than on a diet of *Mytilus edulis*. The growth characteristics of *N. lapillus* depend upon the state of maturity, sex, phenotype and environment, and juvenile animals tend to accumulate shell and body mass faster than adults (Etter, 1988; Burrows & Hughes, 1990; Kirby & Bayne, 1994). Moreover, different sizes and types of prey promote different growth rates in different size predators (Palmer, 1983; Moran et al, 1984).

The higher growth rate observed in individuals of the *N. lapillus* on the *M. edulis* diet and the larger size represented by the *N. lapillus* population that eat *M. edulis* in the field, are probably related to the fact that the handling time for *M. edulis* was shorter (52.7 h) and that the caloric content per individual mussel (1.63 cal) was greater than per individual *L. obtusata* (67.8 h, 0.48 cal) (Chapter 1). The differences in growth rates was probably related to the inherent food value of individuals prey, as the number of prey eaten in each treatment was not significantly different.

The growth rate in Gastropoda is highest in the youngest individuals and commonly declines rapidly with age (Wilbur, 1964; Wilbur & Owen, 1964; Kenny, 1977). Since the growth rate decreases as the individual becomes larger and older, there may be metabolic correlations with size and age (Wilbur & Owen, 1964). Carbonic anhydrase is associated with shell deposition, and a decrease in enzyme activity with age has been related to the decreased rate of shell formation and calcium deposition (Wilbur & Owen, 1964; Zischke et al, 1970). Individuals of *N. lapillus* in the growth experiment (Figure 2.4) showed a decline in the growth rate, although the experiment only lasted 8 months, and *N. lapillus* take about two or two and a half years to become adult (Moore, 1936, 1938; Feare, 1990; Fretter & Graham, 1994). The decrease in relative growth rate in relation to increasing size has been recorded for many mollusks (Wilbur & Owen, 1964; Zischke et al, 1970; Kenny, 1977) and some ceased to grow once they had reached sexual maturity as has been reported for *N. lapillus*, *Cerithium nodulosum*, *Cypraea annulus*, and *C. spadicea* (Moore, 1936, 1938; Feare, 1970; Yamaguchi, 1977; Fretter & Graham, 1994; Darling, 1965; Katoh, 1989).

The fact that *Nucella lapillus* on *Mytilus edulis* and *Littorina obtusata* diets level off at different body sizes, suggests that *N. lapillus* stop growing at a certain age. Etter (1988, 1989)

stated that two different populations of *N. lapillus*, one living in exposed area and the other in a protected area, reached sexual maturity at the same age but at different sizes.

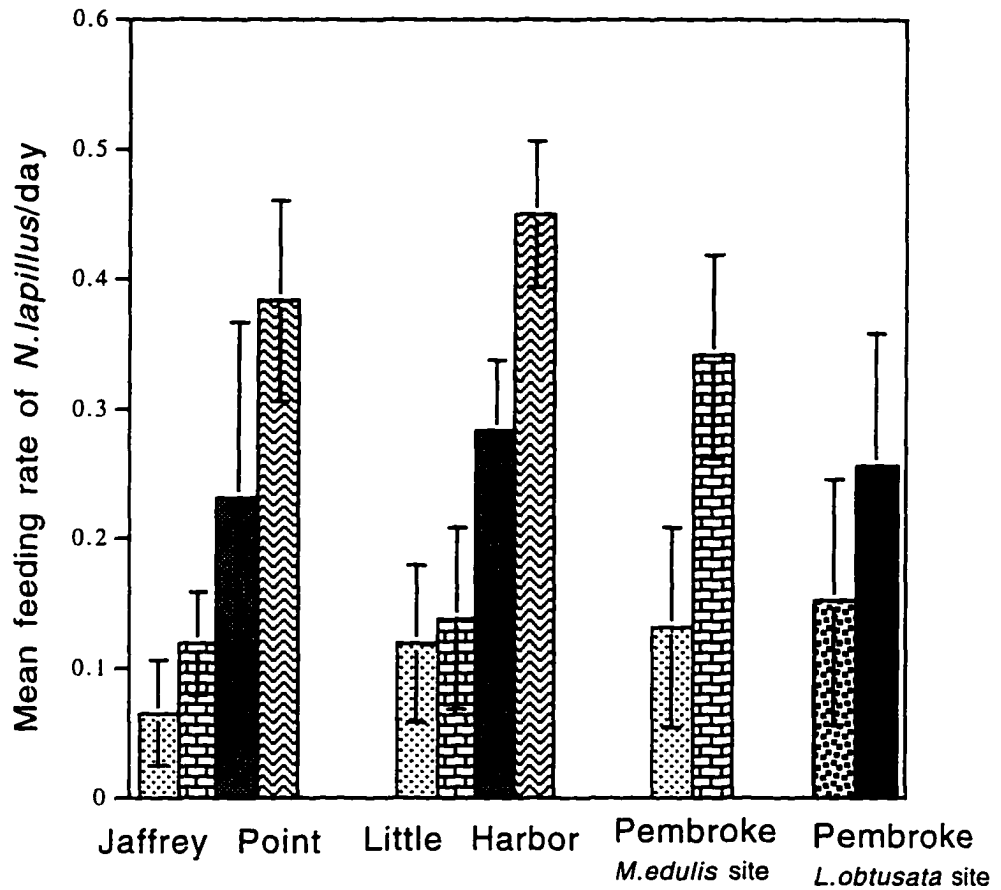
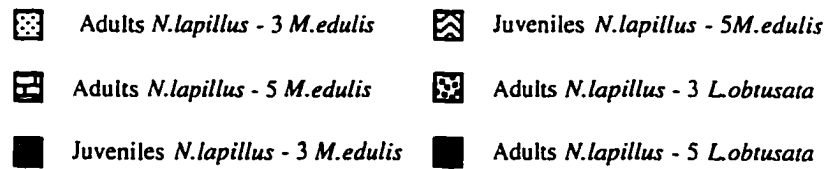


Figure 2.1. Feeding rate of adults and juveniles of *Nucella lapillus* from Jaffrey Point, Little Harbor, NH and adults of *N.lapillus* from Pembroke, Me in two different treatments. Error bars = SD

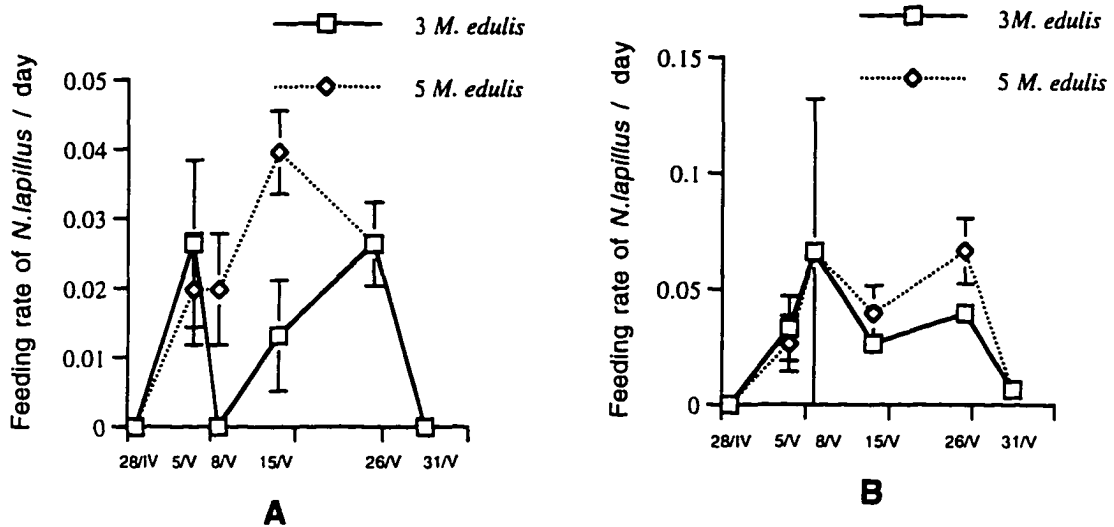
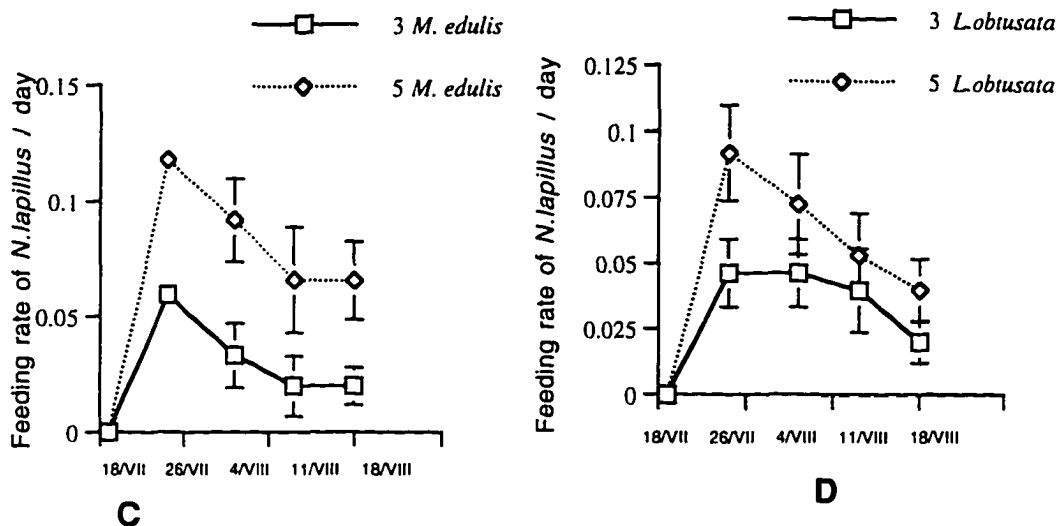
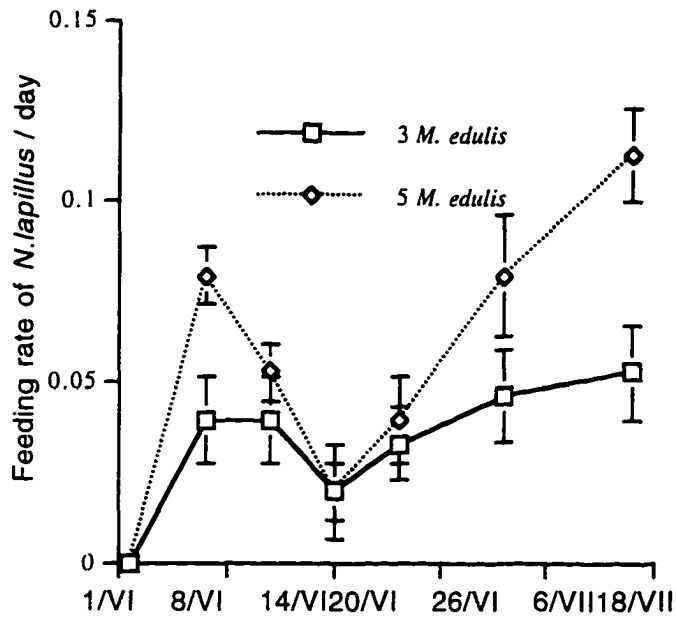


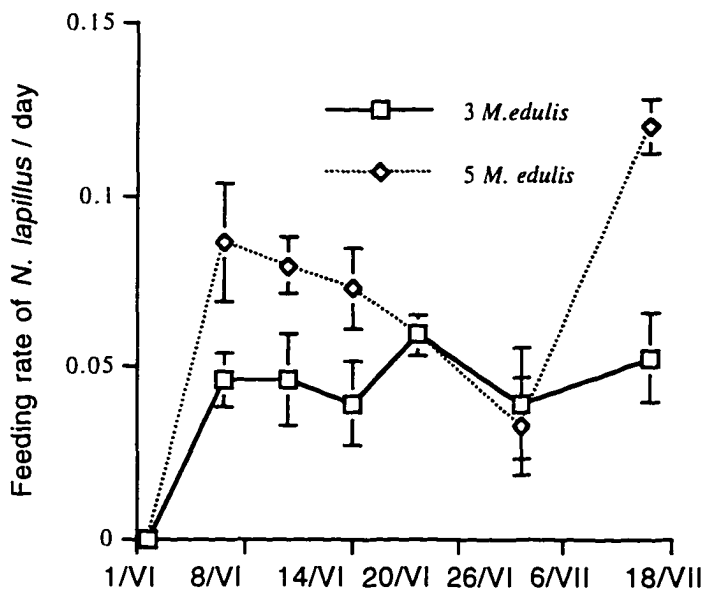
Figure 2.2. Feeding rate of adults individuals of *Nucella lapillus* from Jaffrey Point (A) and Little Harbor (B) in two different treatments, from 28 April to 31 May, 1995. Error bars=SD



Feeding rate of adults individuals of *Nucella lapillus* from two populations from Pembroke (C, D) in two different treatments, from 18 July to 18 August, 1995. Error bars=SD



A



B

Figure 2.3. Feeding rate of juveniles individuals of *Nucella lapillus* from Jaffrey Point (A), and Little Harbor (B) in two different treatments, from 1 June to 18 July, 1995. Error bars= SE

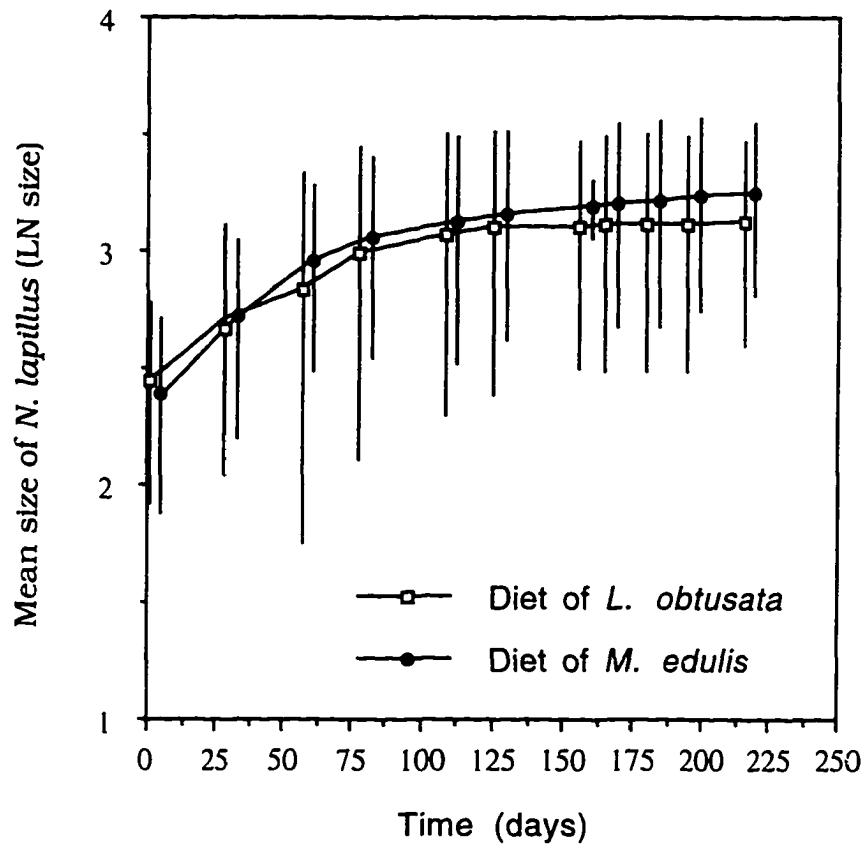


Figure 2.4. growth rate of *Nucella lapillus* from Pembroke, ME in a diet of *Littorina obtusata* and *Mytilus edulis* from 30 May 1995 to 02 January 1996. Data is transformed using a natural log. Bars represent 95% confidence intervals.

CHAPTER III

COMPARISON OF THE PREDATORY BEHAVIOR OF
TWO POPULATIONS OF *Nucella lapillus*
(LINNAEUS, 1758) IN THE PRESENCE OF THE
GREEN CRAB *Carcinus maenas* (LINNAEUS, 1758)

Introduction

The green crab *Carcinus maenas*, originally from Europe, was introduced in North America by the end of the last century (Scattergood, 1952; Glude, 1955; Vermeij, 1978, 1982-b). By 1954, *C. maenas* had been able to extend its range northeastward to Wedgeport, Nova Scotia (Glude, 1955; Taylor, Bigelow & Graham, 1957; Ropes, 1968). Although a decline in sea surface temperatures after 1957 had sharply reduced populations of *C. maenas* in some areas such as the Bay of Fundy (Welch, 1968), the green crab seems to be a well established species in most of the Atlantic Northeast,

and it is considered a very important predator on mollusks.

The impact of *Carcinus maenas* predation on some species of gastropods, has been considered an important selective force in the evolution of the shell. This crab had a great effect on the periwinkle *Littorina obtusata* in the change of the shape of the spire from high to low and in the increase of the thickness of the shell (Trussel,1996). *C. maenas* predation pressure also influenced a thicker shell in the dogwhelk *Nucella lapillus* (Ebling et al,1964; Hughes & Elner,1979; Palmer,1979; Vermeij,1982-a; Hughes,1986). Moreover, the green crab does not just act as a selective force on the evolution of the prey morphology, but it also effects population and community dynamics (Grosholz & Ruiz,1995).

One of the mollusks predated by *Carcinus maenas* is *Nucella lapillus*, which is itself a predator of other benthic mollusks. A population of *N. lapillus* has been closely monitored since 1993 in Pembroke, Maine, where *C. maenas* appeared in obvious numbers in the summer of 1995 (personal observation) . This population of *N. lapillus* prey exclusively on *L. obtusata*, although the latter is not usually a prey of *N. lapillus*. *L. obtusata* is the only prey available to *N. lapillus* in this area over large portions of the intertidal zone. The *L. obtusata* in Pembroke tend to have a high spire indicative of minimal previous crab predation (Trussel, 1996).

When preying on *Littorina obtusata*, *Nucella lapillus*

frequently becomes vulnerable to predation itself, as *L. obtusata* releases from the substratum, and turns both predator and prey lie up side down on the substrate. Based on this apparent vulnerability, it was hypothesized that *N. lapillus* would not usually prey on *L. obtusata* in areas where *C. maenas* is abundant, to avoid predation by this crab.

In order to test this hypothesis, experiments were conducted to determine whether *Nucella lapillus* from the Pembroke population, showed different predation rates on *L. obtusata* in the presence and absence of *C. maenas*. Parallel experiments were also done using *N. lapillus* from the Little Harbor, NH population, where *C. maenas* has been well established and common for over 25 years (L.Harris, personal communication). In another experiment the preference of *C. maenas* between *N. lapillus*, high spire *L. obtusata* and low spire *L. obtusata* was investigated.

Materials and Methods

The animals for all experiments were collected in June and September, 1996 in the following locations: Adults of *Nucella lapillus* (30 - 40 mm in length) in Little Harbor, NH and Pembroke, ME; *Littorina obtusata* (10 - 12 mm in length) with high and low spire in Pembroke and Little Harbor respectively; and *Carcinus maenas* (10 mm or less and 20 - 30 mm in carapace width) in New Castle, NH. All

the animals were transferred to aquaria in a controlled temperature room at 15°C and a salinity of 30‰ at the University of New Hampshire.

Predation Rate Experiment

The experiment on *Nucella lapillus* predation rate on *Littorina obtusata* in the presence and absence of *Carcinus maenas* had two different treatments. In the first treatment, one *N. lapillus* from Pembroke or Little Harbor was placed with five *Littorina obtusata* and one crab in separate cages. The second treatment was similar to the first one, but at this time the crab was placed inside a smaller cage, in order to avoid direct interference on *N. lapillus*. For controls, one *N. lapillus* was placed separately in plastic boxes with just five *L. obtusata*. During the experiment the number of consumed prey by *N. lapillus* was noted and eaten individuals were replaced. Treatments were in separate aquaria to avoid possible chemical cues influencing the results.

The experiment was then repeated, but at this time, the individuals of *N. lapillus* that were exposed to crabs directly in the first test were placed in the treatment where the crabs were caged. Those in the treatment with caged crabs were transferred to the control and those in the control were placed in the treatment with

uncaged crabs. Both experiments lasted one month and each treatment was replicated ten times.

Prey Preference Experiment

The experiment that investigated *Carcinus maenas* prey preferences had also two different treatments: in the first treatment one *Nucella lapillus* from Pembroke or Little Harbor was placed with two *Littorina obtusata*, one with high spire and other with low spire and one small crab (10 mm or less in carapace width) in separate boxes. The second treatment was similar to the first one, but at this time the crab used was 20 - 30 mm in carapace width (large crab). During the experiments the number of consumed prey were noted and eaten individuals were replaced. This experiment lasted for one week and was replicated five times for each population.

Differences in Shell Morphology

The shell thickness of 282 high spire individuals of *Littorina obtusata* from Pembroke, Maine, was compared with the shell thickness of 161 low spire individuals from New Castle, New Hampshire. The thickness of the shell lip was measured in two points: adjacent to the whorl, and at the point opposite to it (Trussell, 1996).

Specimens of *L. obtusata* collected in Massachusetts, New Hampshire, Maine and Canada in the late eighteenth century and again in this century, and deposited in the malacological collection of the Museum of Cultural and Natural History, Harvard University, were examined for possible bore holes. The presence of bore holes in these individuals would indicate possible predation by *Nucella lapillus*.

Results

The results of *Nucella lapillus* predation on *Littorina obtusata* under different exposures to *Carcinus maenas* are summarized in Figure 3.1A and B. In most cases, the predation on *L. obtusata* was significantly higher in the treatments with *Nucella lapillus* from Pembroke than in those with *N. lapillus* from Little Harbor, in both times that the experiment was performed. The difference was not statistically significant for the first trial of controls (Figure 3.1A). *N. lapillus* from Little Harbor did not show a significant variation in its *L. obtusata* predation rate among the two different treatments and the control, in any of the two times that the experiment was performed (Figure 3.1A and B). In contrast, *N. lapillus* from Pembroke showed significantly higher predation rate ($p=0.03$) in the presence of a free crab inside the box, than in the control, where there was no crab (Figure 3.1A). It seems that for *N.*

lapillus from Pembroke, the presence of *Carcinus maenas* may stimulate predatory activity.

Small *Carcinus maenas* were just able to prey on *Littorina obtusata* with high spires, and the predation rate in one of the treatments was significantly higher than zero ($p=0.01$) (Figure 3.2A). They did not attack low spire *L. obtusata* or *N. lapillus*. Large crabs were able to prey on all three food items, and in both treatments high spire *L. obtusata* were successfully attacked most often. The high spire *L. obtusata* predation rate was significantly higher than the low spire *L. obtusata* and *N. lapillus* predation rates in the treatment with *N. lapillus* from Pembroke ($p<0.01$) (Figure 3.3B). In the treatment with *N. lapillus* from Little Harbor the predation rate over high spire *L. obtusata* was also higher than low spire *L. obtusata* but the difference was not statistically significant (Figure 3.3A).

The shell thickness of low spire *Littorina obtusata* was significantly greater than for high spire *L. obtusata* ($p<0.0001$) (Table 3.1). This highly significant difference could be considered an adaptation to protect against crab predation.

The survey of *Littorina obtusata* at the malacological collection of the Natural History Museum of the Harvard University, resulted in finding some shells with bore holes from the late 1800's and early 1900's. Only samples from Maine and Canada had bore

holes. This could be an indication that in the more southern locations, the presence of *Carcinus maenas* was already disturbing the *Nucella lapillus* predation on *L. obtusata*. A limiting factor in this survey of samples was the fact that most specimens were collected alive. In the same collection most specimens of *L. obtusata* had a high spire. Low spire *L. obtusata* were collected as early as 1911 in Massachusetts, and high spire *L. obtusata* were collected as late as 1963 in Massachusetts, Maine and Canada.

Discussion

Foraging decisions can be influenced by several variables independent of energetic returns, such as the presence of a predatory organism that could affect the behavior of the foraging species (Vadas et al. 1994). The decision to forage for *Nucella lapillus* could be critical to survival and it may remain inactive during unfavorable conditions to avoid mortality risk (Burrows & Hughes, 1989).

In the present study, predation on *Littorina obtusata* by *Nucella lapillus* was not inhibited by the presence of the predator *Carcinus maenas* (Figure 3.1A and B). Such results do not support the hypothesis that *N. papillus* does not prey on *L. obtusata* when other prey are available, due to the selection pressure represented by predation by *C. maenas*. However, Vadas et

al (1994) registered that *N. lapillus* put in the presence of predator cues (crabs), responded to the stimulus by remaining inactive.

The higher predation activity by *Nucella lapillus* when in the presence of *Carcinus maenas*, observed in the present study, for the Pembroke population in one of the treatments, (Figure 3.1A) might have been caused by an increase in the stimulus for predation. One possible explanation would be that the presence of *C. maenas* increases the activity by *L. obtusata*, which would lead to an increase in metabolic residues from this prey, and increase the chance of encountering *N. lapillus* that would act as a stimulant to predation. According to Carriker (1981) the chemical stimulus that guides predator gastropods to prey are the metabolic products of prey. Another possibility would be that *N. lapillus* was responding to the overall increase in the concentration of organic metabolites in the water due to the presence of the crabs.

The higher predation rate on *Littorina obtusata* by *Nucella lapillus* from Pembroke in comparison with *N. lapillus* from Little Harbor, is probably a consequence of the different amounts of experience with this particular prey represented by this population. In the Pembroke population area, *L. obtusata* is the primary prey available, whereas in the Little Harbor population area, there are other prey such as *Mytilus edulis*, which is preferred by *Nucella lapillus* over *L. obtusata* (Chapter 1).

The higher predation rate by *Carcinus maenas* on high spire *L. obtusata* over low spire *L. obtusata* and *N. lapillus* is probably a consequence of the higher vulnerability of the former. *L. obtusata* with high spire are easier to hold and have a thinner shell than *L. obtusata* with low spire. Moreover, *C. maenas* has a short persistence time, rejecting the unbroken shell after about three minutes of trying (Hughes & Elner, 1979, Lawton & Hughes, 1985, Rangeley & Thomas, 1987). This way *C. maenas* could do a selection against weaker shells by adopting a foraging strategy of attacking all encountered prey but quickly rejecting those hard to break (Hughes & Elner, 1979). Vermeij (1978) reported that *C. maenas* can break the spire of a gastropod shell, although this is not typical for temperate crabs.

The preference by *Carcinus maenas* on *Littorina obtusata* over *Nucella lapillus* was probably due to the fact that *N. lapillus* were larger than *L. obtusata*. Moreover, Vermeij (1979), states that neogastropod radiations may have evolved under intensive predation by crushing, and as a consequence, neogastropods such as *N. lapillus* have lower frequencies of breakage than archaeogastropods and mesogastropods.

The higher predation rate suffered by individuals of *L. obtusata* with high spires and thinner shells, in comparison with that suffered by individuals with low spires and thicker shells, also

suggests that selection pressure resulted from *C. maenas* predation was responsible for the shortening of the spire, and for the increase in the thickness of the shell in the *L. obtusata* populations that are sympatric to *C. maenas*. Trussell (1996) reported that *L. obtusata* populations that are sympatric to this crab have thicker shells than those that are not.

The reduced predation by juvenile *Carcinus maenas* on high spire *Littorina obtusata* and no predation on low spire *L. obtusata* and *N. lapillus* is in agreement with the Rangeley and Thomas (1987) who found that juvenile *C. maenas* prey mainly on barnacles, whereas the adults prey mainly on gastropods.

The conspicuous increase in the numbers of green crabs in the Pembroke area in 1995 may lead to the appearance of shorter spires and thicker shells in the *L. obtusata* population. These morphological modifications may appear as a result of an evolutionary process, as the local adaptation rate in this species is thought to be high, due to a low gene flow between populations caused by the absence of a planktonic larvae (Currey & Hughes, 1982, Vermeij, 1982-a, Reimchen, 1982). On the other hand, shorter spires and thicker shells may also become a result of the phenotypic plasticity of the population. Trussell (1996) demonstrated that *L. obtusata* exhibit an increase in the thickness of the shell, when grown in the presence of the green crab, and Palmer (1990) reported

that *N. lapillus* exposed to the effluent of crabs produced heavier shells with thicker lips and more well-developed apertural teeth.

Although the changes in shell morphology observed in *Littorina obtusata* and *Nucella lapillus* following the introduction of *Carcinus maenas*, have been interpreted as the result of microevolutionary change (Vermeij, 1982-b, Seeley, 1986), they could equally have been an ecophenotypic response to the presence of the crabs (Appleton & Palmer, 1988, Palmer, 1990). Morphological differences among natural populations may also be a result of the combination of environmental and genetic effects. The monitoring of the Pembroke population would be a good test case to observe if the increase in the green crab density will be followed by changes in the *Littorina obtusata* and *Nucella lapillus* morphology.

Table 3.1. Thickness of *Littorina obtusata* shell measured in two points: adjacent to the whorl (a), and at the point opposite to it (b).

	Low spire <i>L. obtusata</i> (a)	High spire <i>L. obtusata</i> (a)
Mean:	1.8	0.85
Std error:	0.02	0.01
N:	161	282

	Low spire <i>L. obtusata</i> (b)	High spire <i>L. obtusata</i> (b)
Mean:	1.1	0.48
Std error:	0.02	0.008
N:	161	282

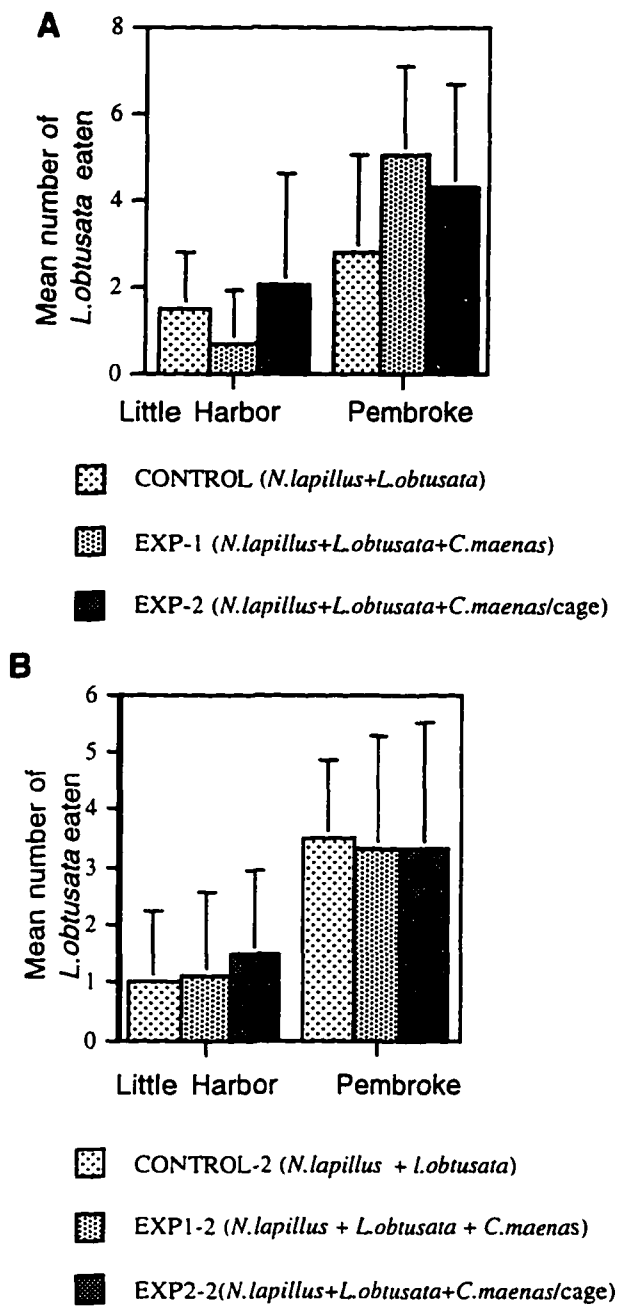


Figure 3.1. Mean number of *Littorina obtusata* eaten by two populations of *Nucella lapillus* in the presence of *Carcinus maenas* in two different experiments (A-first time, B-second time). Error bars=SD

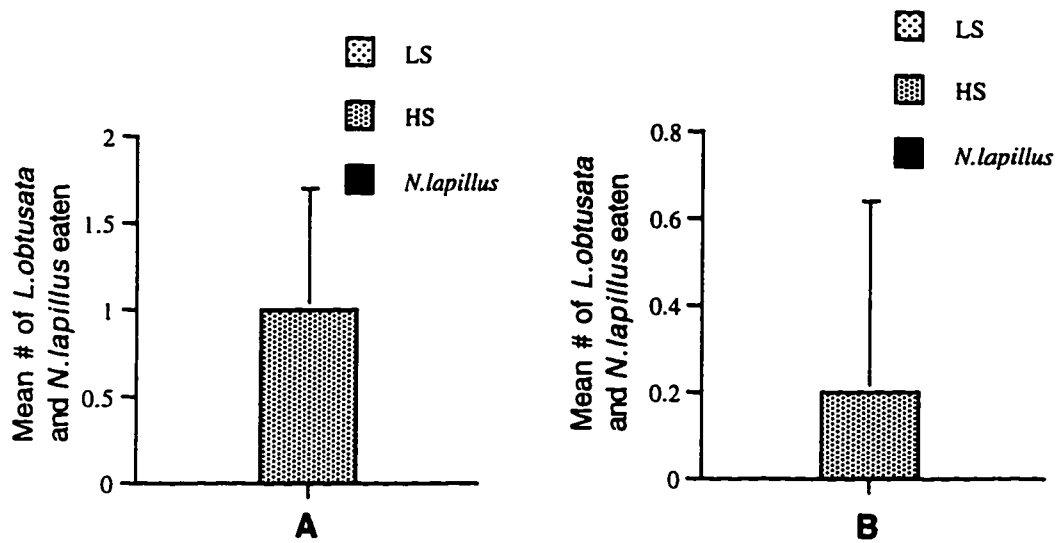


Figure 3.2. Mean number of *Nucella lapillus* (A- from Little Harbor, NH B- from Pembroke, Me), low spire *Littorina obtusata* (LS) from Little Harbor, high spire *Littorina obtusata* (HS) from Pembroke preyed by small *Carcinus maenas* (10 mm or less carapace width). Error bars=SD

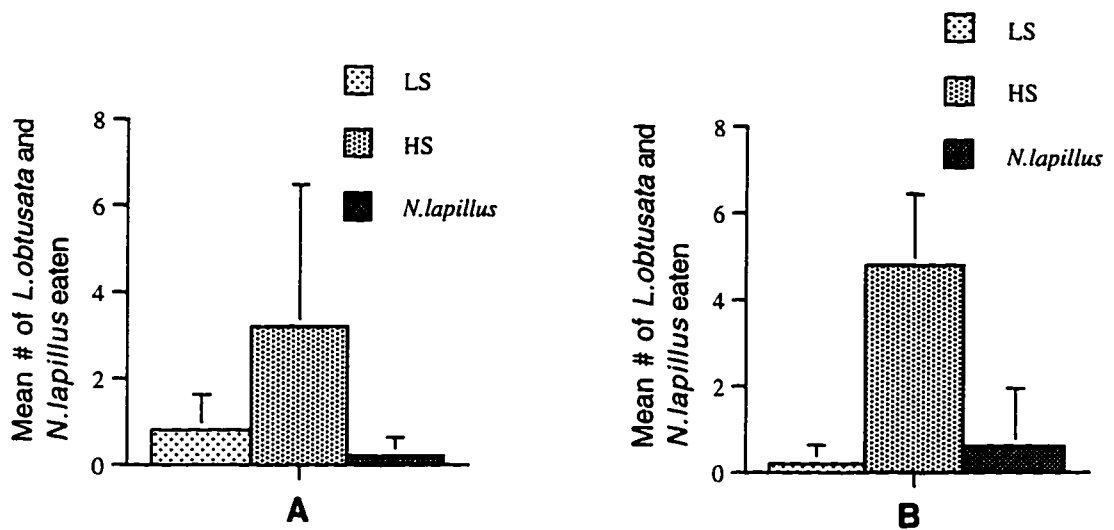


Figure 3.3 Mean number of *Nucella lapillus* (A- from Little Harbor, NH B- from Pembroke, Me), low spire *Littorina obtusata* (LS) from Little Harbor, high spire *Littorina obtusata* (HS) from Pembroke preyed by big *Carcinus maenas* (20-30 mm carapace width). Error bars=SD

GENERAL CONCLUSIONS

Nucella lapillus is a intertidal prosobranch that usually preys on the mussel *Mytilus edulis* and on the barnacle *Semibalanus balanoides*, but occasionally also on the periwinkle *Littorina obtusata*. This dissertation in the Chapter one has shown that the maintenance of *Nucella lapillus* on a single diet, would reinforce a existing preference for this prey (ingestive conditioning), but would not form a preference for it. The ability of *N. lapillus* to recognize a new kind of prey, depends of a learning process (ingestive conditioning), which is trigger by the scarcity in abundance of the preferred prey *Mytilus edulis* .

Adult and juveniles individuals of *Nucella lapillus* in the Chapter two showed a higher feeding rate when more prey were available. This increase in feeding rate with prey density may represent a non-adaptative response to the increase in the concentration of chemosensory or tactile cues of prey presence, as *Nucella lapillus* is a nonvisual predator relying entirely on chemosensory or tactile cues. On the other hand, such a predator response to an increase in prey abundance may also represent an adaptative response, as an increase in prey abundance can reduce predation costs related to capture, competition, and risk of

predation.

Results obtained in the present study, indicate that *Mytilus edulis* has greater potential "food value" than *Littorina obtusata*. *Nucella lapillus* showed a higher growth rate feeding on *Mytilus edulis* than on *Littorina obtusata*, and the mean size of the individuals of *Nucella lapillus* measured in the field was higher in the population that preyed on *Mytilus edulis* than in the population that fed on *Littorina obtusata* (Chapter two). Moreover, *M. edulis* presented higher caloric content per individual and required a shorter handling time to *N. lapillus* than *L. obtusata* (Chapter one).

The green crab *Carcinus maenas* is a predator on mollusks, that appeared for the first time in the summer of 1995 in obvious numbers in Pembroke, Maine. Experiments in Chapter three showed that predation on *L. obtusata* by *Nucella lapillus* from Pembroke and from Little Harbor, NH (where the green crab has been well established), was not inhibited by the presence of the predator *C. maenas*. *Nucella lapillus* had rather, a higher predation activity when in the presence of *Carcinus maenas*. One possible explanation would be that the presence of *C. maenas* increases the activity by *L. obtusata*, which would lead to an increase in metabolic residues from this prey that would act as a stimulant to predation, and / or to an increase of the chances of encountering *N. lapillus*. Another possibility would be that *N. lapillus* was responding to the overall

increase in the concentration of organic metabolites in the water due to the presence of the crabs.

Carcinus maenas preferred *Littorina obtusata* with high spires over *Nucella lapillus*, and low spire *Littorina obtusata* in experimental studies (Chapter three). This preference was due probably to the higher vulnerability of *L. obtusata* in relation to *N. Lapillus*, and to the fact that the high spire form of *L. obtusata*, is easier to hold and has a thinner shell than the low spire form. This research represents a contribution in the understanding of the trophic relations between these important components of New England intertidal communities.

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