

PREY PREFERENCE AND RECOGNITION BY *Nucella lapillus* (LINNAEUS, 1758) (MOLLUSCA: GASTROPODA)¹

Preferência e reconhecimento de presas por *Nucella lapillus*
(Linnaeus, 1758) (Mollusca: Gastropoda)

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RESUMO

Preferência e reconhecimento de presas por indivíduos de Nucella lapillus de 13 populações da Nova Inglaterra (USA) foram estudadas para determinar se, ao permanecerem numa dieta única, desenvolvem uma preferência por essa presa e se a disponibilidade de presa afeta reconhecimento por esse predador. Os experimentos duraram um mês para cada população. Cada N. lapillus foi colocado com 5 ou 10 presas dependendo do experimento os quais foram replicados 10 vezes. Indivíduos das 13 populações mostraram preferência por Mytilus edulis sobre Littorina obtusata em experimentos no laboratório, inclusive uma população de N. lapillus que se alimenta exclusivamente de L. obtusata no campo. Indivíduos de uma população de N. lapillus não foi capaz de reconhecer L. obtusata como presa. N. lapillus permanecendo numa dieta de M. edulis no laboratório teve sua preferência por essa presa reforçada, mas indivíduos de N. lapillus em dieta de L. obtusata, não desenvolveram uma preferência por essa presa. O menor tempo de forrageamento e o maior conteúdo calórico explicariam a preferência por M. edulis sobre L. obtusata.

Palavras-chaves: predação, preferência, comportamento, Mollusca, Gastropoda.

ABSTRACT

Prey preference and recognition by individuals from 13 populations of Nucella lapillus (Linnaeus, 1758) from New England (USA) were studied to determine if individuals fed a single prey diet develop a preference for this prey, and if prey availability affects prey recognition. Individuals from all populations showed a preference for Mytilus edulis over Littorina obtusata in laboratory experiments, including those that prey just on L. obtusata in the field. Individuals from one other population were not able to recognize L. obtusata as 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.

Key words: predation, preference, behavior, Mollusca, Gastropoda.

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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 large. 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 small search times, specialization is favored (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 become 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 with the density of the available prey. In other cases, preference for one prey type depends on the relative density of prey types available, and hence 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 additional to the more immediate effects of learning called ingestive conditioning (Hughes, 1986). 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. That species has intracapsular metamorphic development (no free larval stage) with newborn hatching out of an egg capsule as juvenile snails (Fretter & Graham, 1994). *N. lapillus* also has very limited movement and, according to Connell (1961) it moves, on average, 10 cm during one tidal cycle, and

no more than 30 meters in a lifetime (Castle & Emery, 1981). As a consequence, each local population is isolated and there is little, or no interchange of genes between them.

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, USA. In one beach of the Maine coast, a population of *N. lapillus* was found feeding just on *Littorina obtusata* which usually is not one of the main prey of *N. lapillus*. The 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.

MATERIAL AND METHODS

Study Areas

The areas studied in this paper are located in the Gulf of Maine, a partially enclosed sea extending from Nantucket Shoals and Cape Cod, Massachusetts (70°W, 42°N) to Cape Sable, Nova Scotia (65°W, 43.5°N). A complex association of igneous metamorphic rocks establish the geology of most strata, that is of late Precambrian and Paleozoic ages (Mathieson *et al.*, 1991).

The study sites were located at Halibut Park, Cape Ann, Massachusetts (42°41'N, 70°38'W); Hilton Park (43°07'N, 70°50'W), Jaffrey Point (43°03'N, 70°43'W), Little Harbor (43°03'N, 70°43'W), New Hampshire; Boothbay Harbor (43°51'N, 69°38'W), two populations from Pembroke separated by about one hundred meters from each other, that show different behavior, one preying on *Littorina obtusata* (Pembroke / LO), and the other preying on *Mytilus edulis* (Pembroke / ME) (44°52'N, 67°13'W), Reversing Falls (44°52'N, 67°13'W), Rockland (44°06'N, 69°06'W), Schoodic Point (44°20'N, 68°05'W), Spruce Head (44°00'N, 69°07'W), West Quoddy Head (44°49'N, 69°59'W), and Winter Harbor (44°20'N, 68°05'W), Maine.

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:

Halibut Park - extremely exposed (EI = 1): *Mytilus edulis* is common in the lower mid littoral as very tiny crowded individuals, and *Nucella lapillus* has short spire and large aperture.

Hilton Park - fairly sheltered (EI = 5): *Semibalanus balanoides* and *Nucella lapillus* are common in the mid littoral.

Jaffrey Point - semi-exposed (EI = 4): the dominant algae are *Fucus* sp. and *Ascophyllum* sp. and the dominant animals are *Semibalanus balanoides* (Annala, 1974; Mathieson *et al.*, 1981; Hardwick-Witman & Mathieson, 1983), and *Nucella lapillus* is common on the open rock.

Little Harbor - sheltered (EI = 6): *Semibalanus balanoides*, *Littorina obtusata* and *Nucella lapillus* are common in the mid littoral.

Boothbay Harbor - fairly sheltered (EI = 5): *Semibalanus balanoides* and *Nucella lapillus* are common and *Littorina obtusata* is frequent on the fucoids in the mid littoral.

Pembroke/LO - very sheltered (EI = 7): *Littorina obtusata* is abundant on *Ascophyllum* sp that covers most of the mid littoral, and *Nucella lapillus* has a long shell.

Pembroke/ME - very sheltered (EI = 7): *Mytilus edulis* is common as groups of large specimens, *Littorina obtusata* is abundant and *Nucella lapillus* has a long shell.

Reversing Falls - exposed (EI = 3): *Mytilus edulis* is abundant and *Nucella lapillus* is common.

Rockland - fairly sheltered (EI = 5): *Semibalanus balanoides*, *Littorina obtusata* and *Nucella lapillus* are common.

Schoodic Point - very exposed (EI = 2): *Semibalanus balanoides*, *Mytilus edulis* are common and *Nucella lapillus* has a short spire and large aperture.

Spruce Head - very sheltered (EI = 7): *Semibalanus balanoides*, *Mytilus edulis*, and *Littorina obtusata* are common, and *Nucella lapillus* has a long shell.

West Quoddy Head - semi-exposed (EI = 4): *Semibalanus balanoides* and *Nucella lapillus* are common.

Winter Harbor - sheltered (EI = 6): *Semibalanus balanoides*, and *Nucella lapillus* are common in the mid littoral.

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 *Nucella*. The first experiment was performed in four populations (Jaffrey Point, Little Harbor, Pembroke / LO and Pembroke / ME) and the second one in all thirteen 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 plastic boxes. Each *N. lapillus* was placed with five individuals of *Mytilus edulis* and five of *Littorina obtusata*. As 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 *L. obtusata* and *M. edulis* consumed was calculated for each the *Nucella lapillus* population. The same experiment was also done with juveniles of the four populations but with just 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 *M. edulis*. *N. lapillus* from twelve 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 twelve 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 temperature of 8 °C (four populations) and 15 °C (all 13 populations).

Considering that the West Quoddy Head site is a very heterogeneous area, the experiments in recognition with this population were done two times. 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 of *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) and used to calculate the energy obtained per prey consumed. These results were then used to compare the relative value of each prey type.

To measure the prey availability in these sites, 0.10 m²-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.

RESULTS

Preference

Both adult and juvenile individuals of *Nucella lapillus* from all four populations showed a preference for *Mytilus edulis*, during the one-month experiment, consuming a greater number of this prey than of *Littorina obtusata*. 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 and 2). The difference in the numbers of prey eaten among populations was statistically significant ($P < 0.001$).

Recognition

All 13 populations studied were able to recognize *Littorina obtusata* as prey except the population from Jaffrey Pt., New Castle, NH (Figures 3 and 4). 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 4). The difference in the number of individuals that recognized prey among populations was statistically significant ($P < 0.025$ at 8 °C and $P < 0.001$ 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 of sheltered areas than in the populations of exposed areas ($P < 0.001$). Among the seven sheltered beaches the percentage of recognition of *L. obtusata* as food by indi-

viduals of *N. lapillus* was highest in Boothbay Harbor, where the more abundant prey was *Semibalanus balanoides*. Among the five exposed beaches the percentage of recognition of *L. obtusata* as prey by individuals of *N. lapillus* was highest in Halibut Park, where the more abundant prey was *Mytilus edulis* whose individuals, however were very small, probably due to the high wave action (Figure 5). Some individuals of *N. lapillus* from the population of Halibut Park were observed successfully preying on *L. obtusata* by the aperture instead of drilling through the shell.

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 prey, probably for having prior 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*, namely the dorsal side between the spire and the body whorl (Lull, 1979), but rather drilled the bore hole in different sites on the body whorl. Nevertheless, after eating 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.

Mytilus edulis was significantly more abundant in exposed areas than in sheltered areas ($P < 0.017$). 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 6). Although sheltered areas showed a higher percentage of recognition 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) than when it preyed on *M. edulis* (52.7 h) (Figure 7). 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 - 20mm in length) than *L. obtusata* (10 - 12mm in length) the mean caloric content per individual was higher for the former (1.63 cal) than for the latter (0.48 cal).

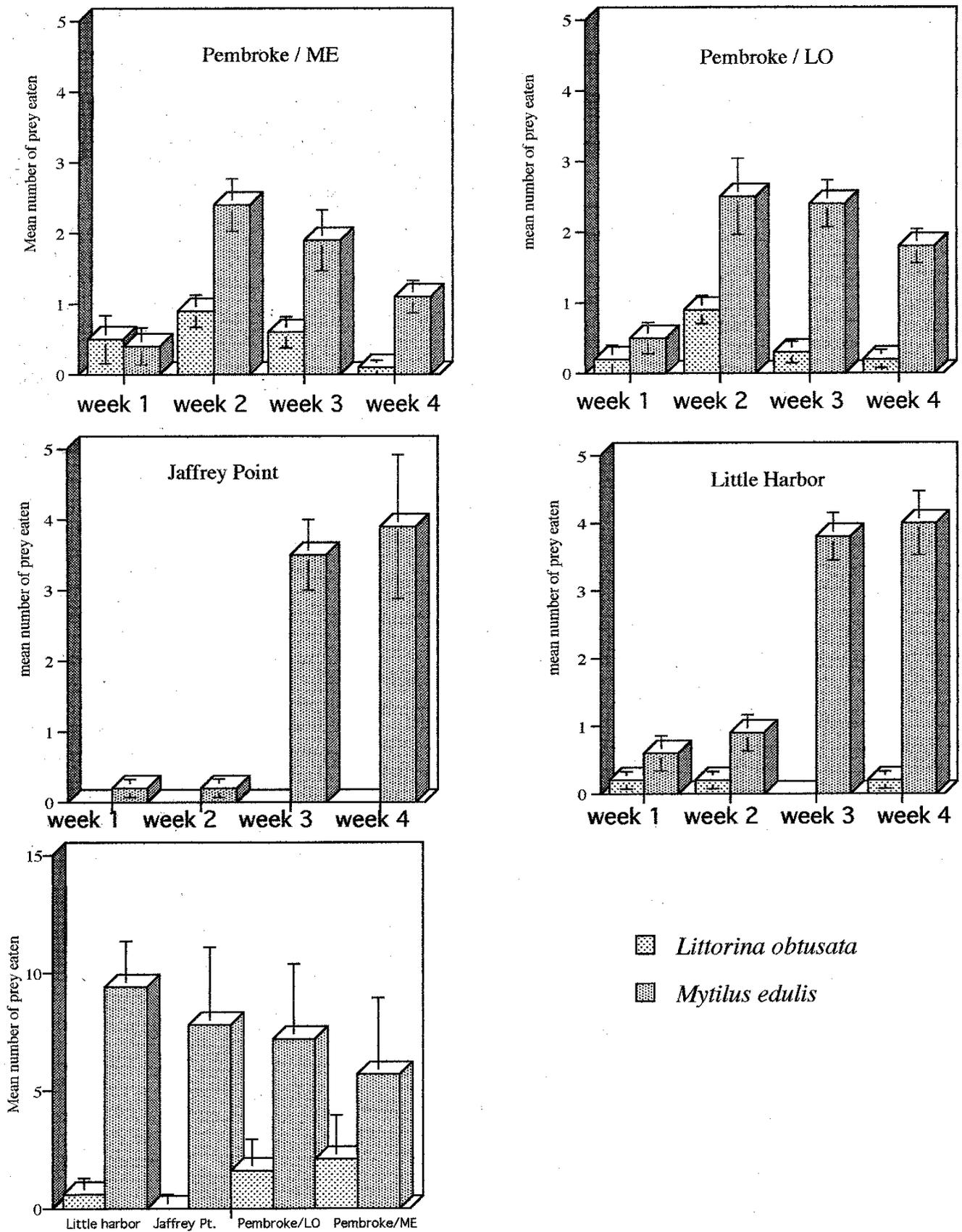


Figure 1 - Mean number of individuals of *Littorina obtusata* and *Mytilus edulis* eaten by one adult individual of *Nucella lapillus* from four different populations during a 30-day period experiment. Error bars=SD.

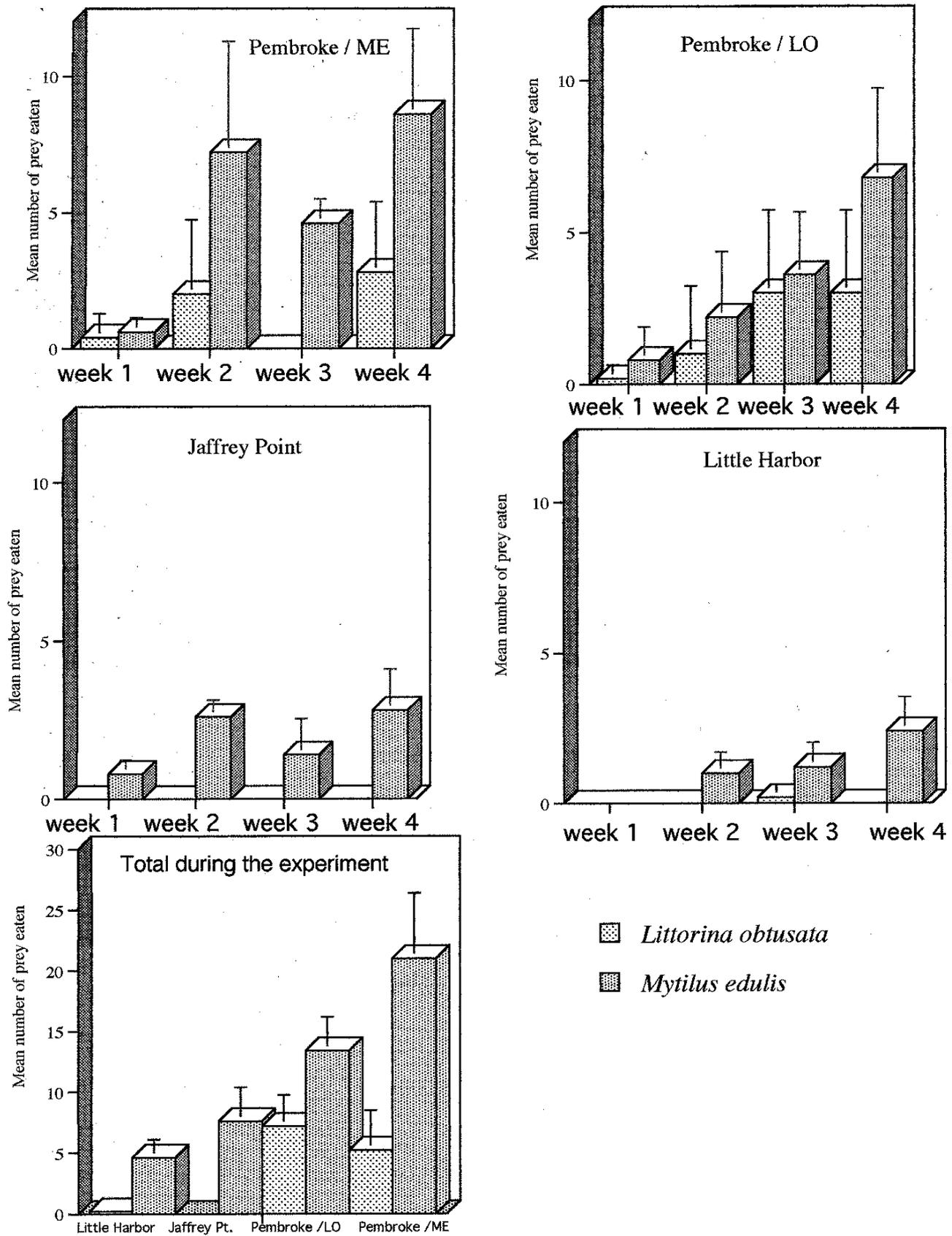


Figure 2 - Mean number of individuals of *Littorina obtusata* and *Mytilus edulis* eaten by one juvenile individual of *Nucella lapillus* from four different populations during a 30-day period experiment. Error bars=SD.

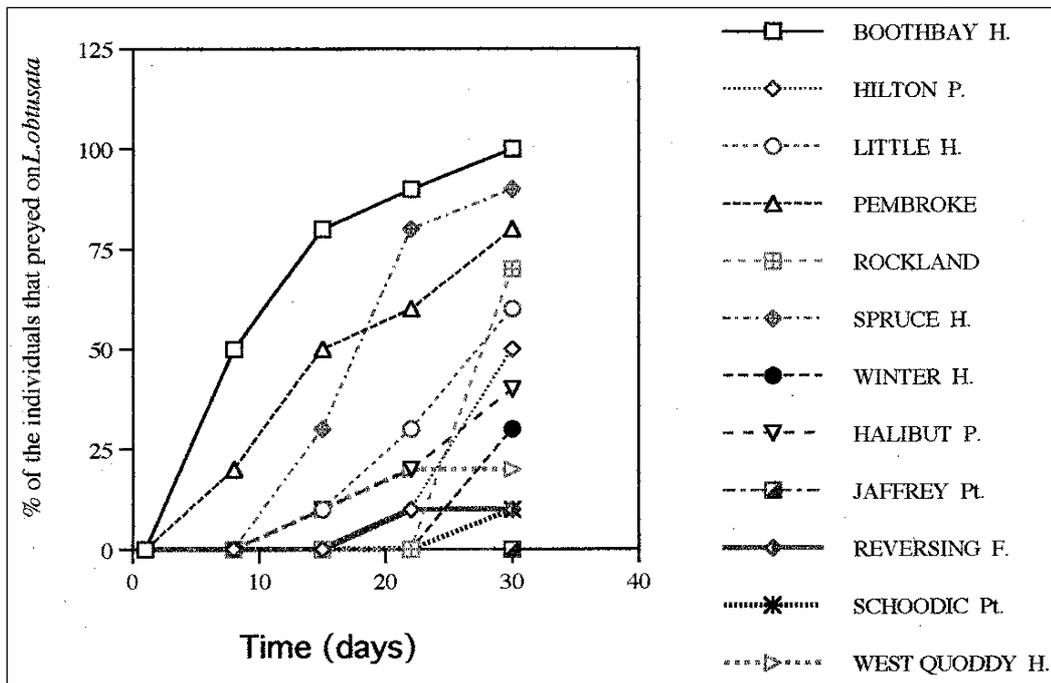


Figure 3 - Cumulative percentage of individuals (N=10) of *Nucella lapillus* from twelve populations that recognize *Littorina obtusata*, as prey during a 30-day period, at a 15 °C temperature.

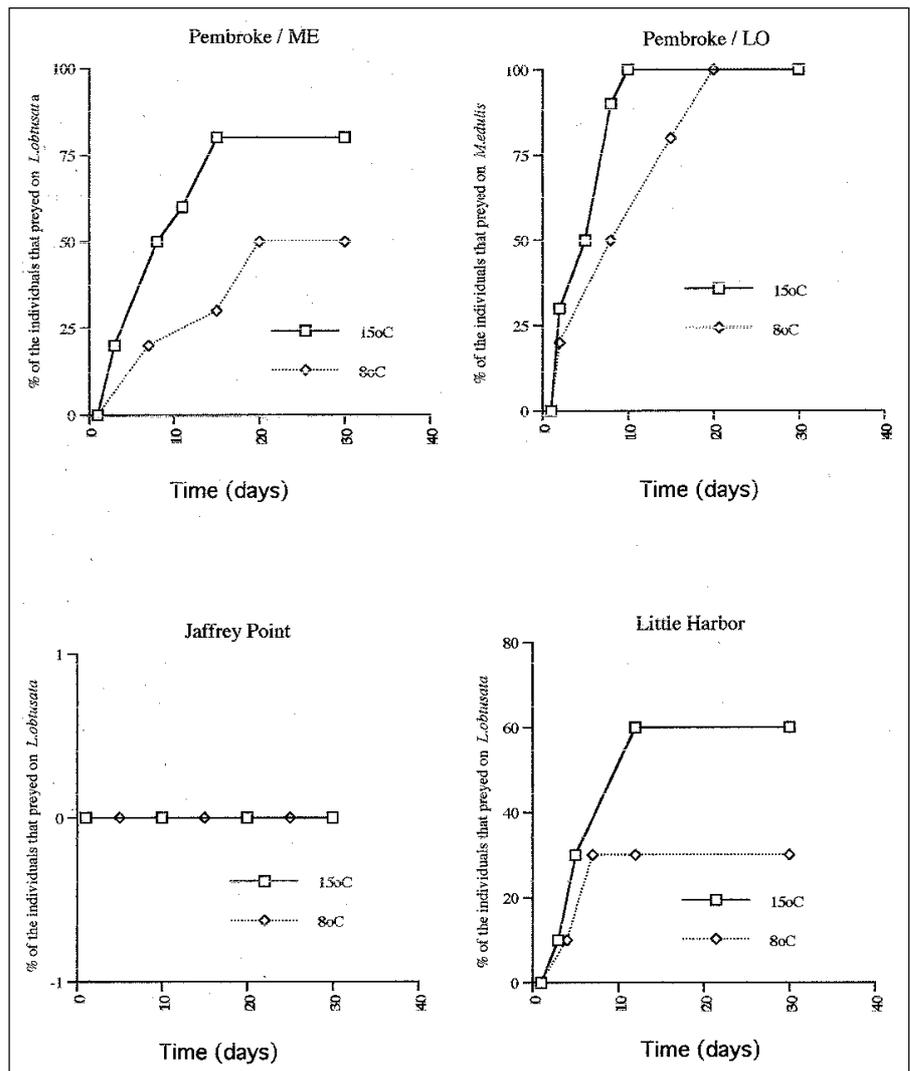


Figure 4 - Cumulative percentage of individuals of *Nucella lapillus* from four populations that recognize new prey during a 30-day period, at 8 °C and 15 °C.

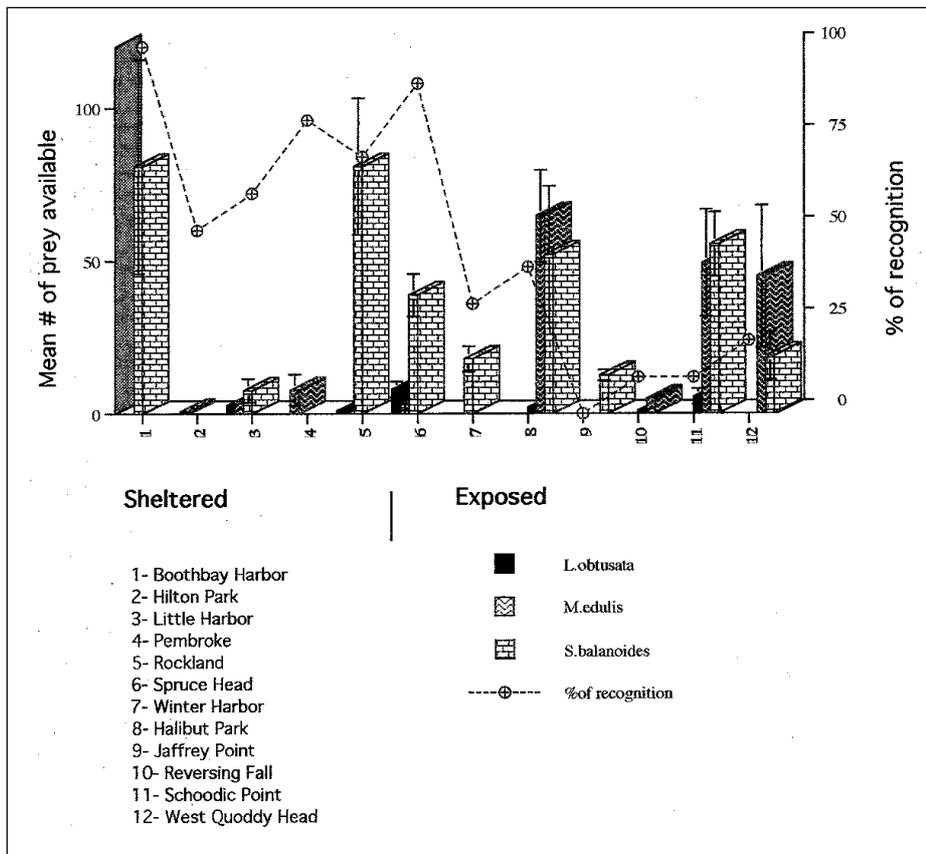


Figure 5 - Mean number of prey available for each *Nucella lapillus* in seven sheltered and five exposed sites during spring, summer and fall, 1994-96, and percentage of *N. lapillus* that recognized *Littorina obtusata* as food.

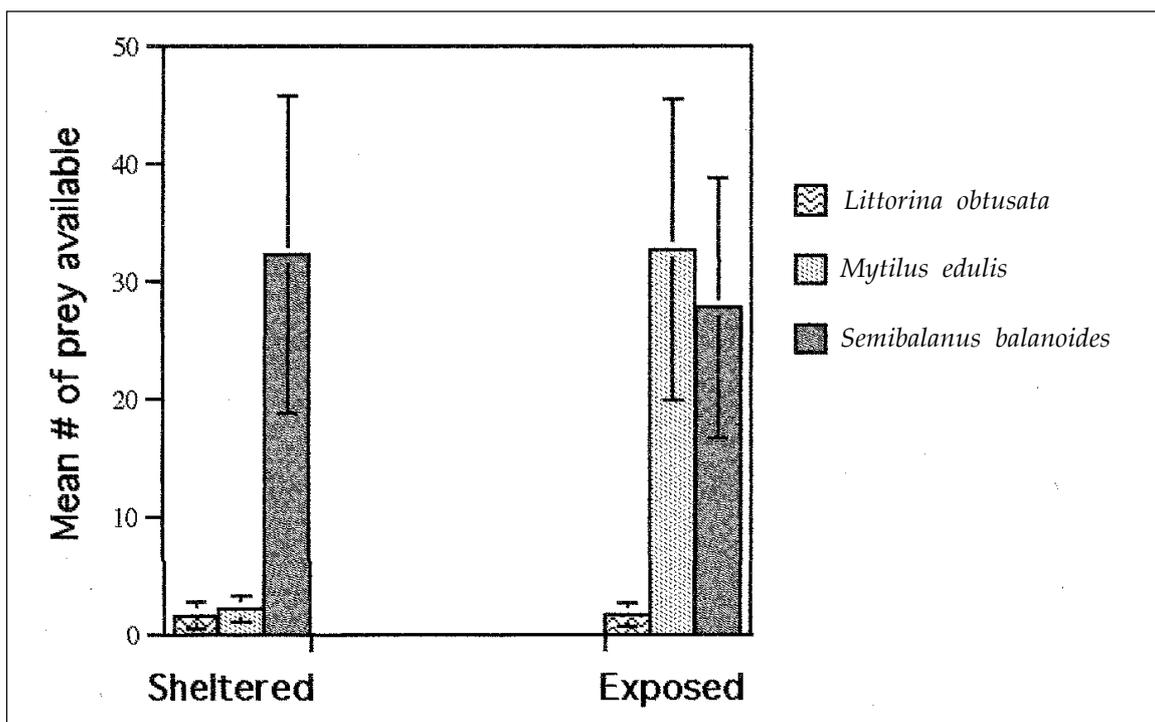


Figure 6 - Mean number of prey available for *Nucella lapillus* in all seven sheltered sites and in all five sites. Error bars=SD.

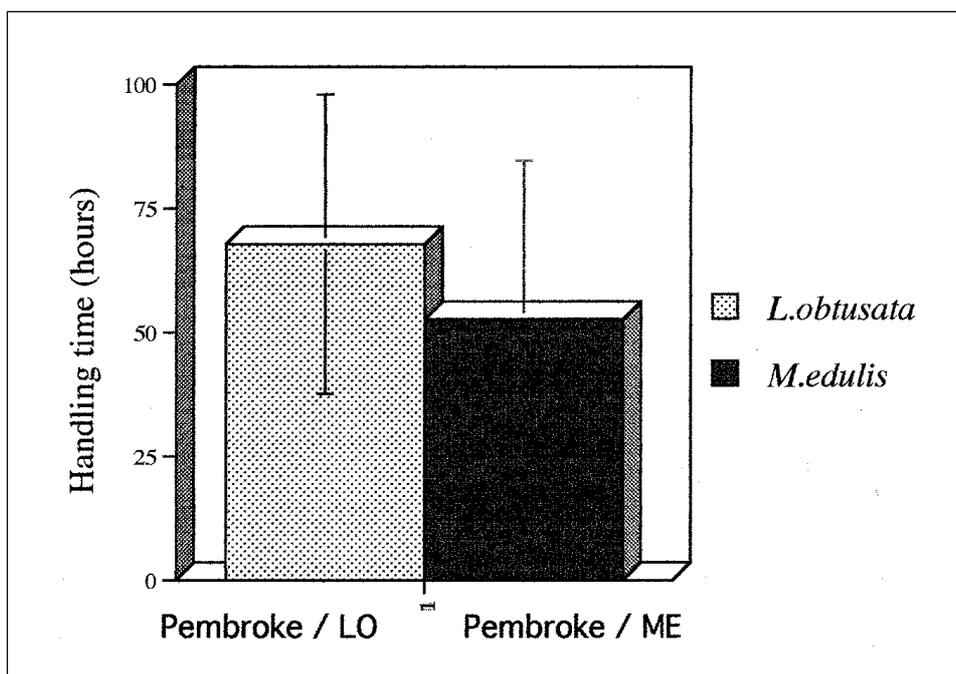


Figure 7- Handling time of individuals from the population Pembroke/LO preying on *Littorina obtusata*, and individuals from the populations Pembroke/ME preying on *Mytilus edulis*. Error bars=SE.

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, which may involve a training process (Hall *et al.*, 1982). In birds, this training is a formation of search image (Royama, 1970; Dawkins, 1971) and in gastropods this training 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, *N. lapillus* from Pembroke/LO that had probably only eaten *L. obtusata* in the field (no mussels and barnacles were found in this site) recognized *M. 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. 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 begins to drill on *M. edulis*, it drills 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.

It seems that *N. lapillus* has the capacity to prey on *L. obtusata* but requires some training to learn how to do it. The recognition of *L. obtusata* as a prey by *N. lapillus* in 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 and 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 study may be due also to chance encounters in the field. West (1988) studied a population of *Thais melones* and found that in the same population some individuals were specialists and others were generalists. According to West (1988) this difference between individuals as maintained by 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).

CONCLUSIONS

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

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