FEEDING RATE AND GROWTH RATE OF Nucella lapillus PREYING ON Littorina obtusata AND Mytilus edulis[1]

Taxa alimentar e taxa de crescimento de *Nucella lapillus* predando *Littorina obtusata* e *Mytilus edulis*

Helena Matthews-Cascon[2]

RESUMO

No presente trabalho foram estudadas a taxa alimentar e a taxa de crescimento de quatro populações de Nucella lapillus *predando* Littorina obtusata *e* Mytilus edulis. *Para testar a hipótese de que as taxas alimentares de* N.lapillus *predando* M. edulis *e* L. obtusata, *são influenciadas pela densidade de presas, indivíduos de* N.lapillus *das quatro populações foram colocados em caixas separadas com três ou cinco presas dentro de tanques com água do mar. Para determinar qual dieta possibilitaria uma maior taxa de crescimento, dois grupos de dez juvenis de uma das quatro populações de* N. lapillus *foram colocadas em caixas separadas, um grupo alimentando-se de* M. edulis *(10-30 mm) e o outro de* L. obtusata *(5-12 mm), durante 8 meses. Adultos e juvenis de* N. lapillus *mostraram uma maior taxa alimentar predando* M. edulis *e* L. obtusata, *nos experimentos com maior densidade de presas. Estes resultados podem representar uma resposta não adaptativa ao acréscimo da concentração de estímulos quimiosensoriais ou táteis devido a maior abundância da presa ou uma resposta adaptativa, já que um aumento na abundância da presa pode reduzir o esforço de predação relacionados a captura, competição e riscos.* N. lapillus *mostrou uma maior taxa de crescimento predando* M. edulis, *de modo que esta espécie se destaca como de maior valor nutritivo.*

***Palavras-chaves*:** Nucella lapillus, Mytilus edulis, Littorina obtusata, *taxa alimentar, taxa de crescimento predação.*

ABSTRACT

In the present study, the feeding and growth rates of four populations of Nucella lapillus *preying on* Littorina obtusata *and* Mytilus edulis *were investigated. In order to test the hypothesis that the feeding rates of* N. lapillus *on* M. edulis *and* L. obtusata, *are influenced by prey density, individuals of all four populations of* N. lapillus *were placed in separate boxes inside water tanks with three or five prey items. To determine which one of the diets allows* N. lapillus *the higher growth rate, two groups of ten juveniles from one of its four populations were placed in separate boxes. One group was fed with* M. edulis *(10-30 mm) and the other with* L. obtusata *(5-12 mm), during an 8 month period. Adults and juveniles of* N. 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. These results may represent a non-adaptive response to the increase in the concentration of chemosensory or tactile cues of prey abundance or an adaptive response, as an increase in prey abundance can reduce the predation effort related to capture, competition and risks.* N. lapillus *showed a higher growth rate feeding on* M. edulis *than on* L. obtusata *so that this species stands out as having a greater "food value".*

***Key words*:** Nucella lapillus, Mytilus edulis, Littorina obtusata, *feeding rate, growth rate, predation.*

[1] Paper produced through a research grant awarded by the Brazilian National Research Council (CNPq) and University of New Hampshire, USA.

[2] ProfessorAdjunto do Departamento de Biologia e Pesquisadora do Instituto de Ciências do Mar, Universidade Federal do Ceará, Campus do Pici, Fortaleza, Brazil. E-mail: hmc@ufc.br

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 one 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). A 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 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 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 the intertidal zone, that preys mainly on the mussel *Mytilus edulis*, on the barnacle *Semibalanus balanoides* (Annala,1974; Menge, 1976; Crothers, 1977), and also on *Littorina obtusata* (Colton, 1916; Moore,1938; Lull,1979).

Early studies have demonstrated a *N. lapillus* preference for *Mytilus edulis* over *L. obtusata* (Matthews-Cascon, 2001). 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 (Matthews-Cascon, 2001).

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 prey.

STUDY AREAS

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 index = 4, according to Ballantine, 1961), with *Fucus* sp., *Ascophyllum* sp. and *Semibalanus balanoides* as the dominant organisms (Annala,1974; Mathieson *et al.*,1981,) and *Nucella lapillus* as abundant on open rock surfaces. Little Harbor is a sheltered site (exposure index = 6, according to Ballantine, 1961) with *Semibalanus balanoides, Littorina obtusata,* and *Nucella lapillus* abundant in the mid littoral. Pembroke is a very sheltered site (exposure index = 7, according to 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 prey density, 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* a 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 measurement of shell length was made at least once a month and the food consumed was replaced once a week, whereby 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 individual sizes of both *Nucella lapillus* populations from Pembroke, in June, 1994, 0.10-m^2 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.

Measurement procedure

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 *N.lapillus* from all four populations showed higher feeding rates in the treatment with five prey than in the one with three prey (Figures 1 and 2), although the difference was statistically significant just in the Pembroke population 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 (Figure 1). 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) is probably due to the satiation of the animals after the first few days, what did not happen among the juveniles probably because the growth process they were undergoing demands increasing amounts of food (Figure 3).

N.lapillus showed a higher growth rate while feeding on *Mytilus edulis* than on *L.obtusata* (P<0.001) (Figure 4). The difference in growth rate was already evident two months after the beginning of the experiment (Figure 4). The mean number of *M. edulis* eaten per predator (41.6 ± 5.34, range 33-50, N=10) was not significantly different from the number of *L. obtusata* eaten per predator (42.0 ± 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 ± 1.21mm, 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 ± 6.00 mm, range 8-33.1 mm, 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 mm, 5-33.1 mm, N = 87). Both results indicate that *M. edulis* has greater "food value" than *L. obtusata*.

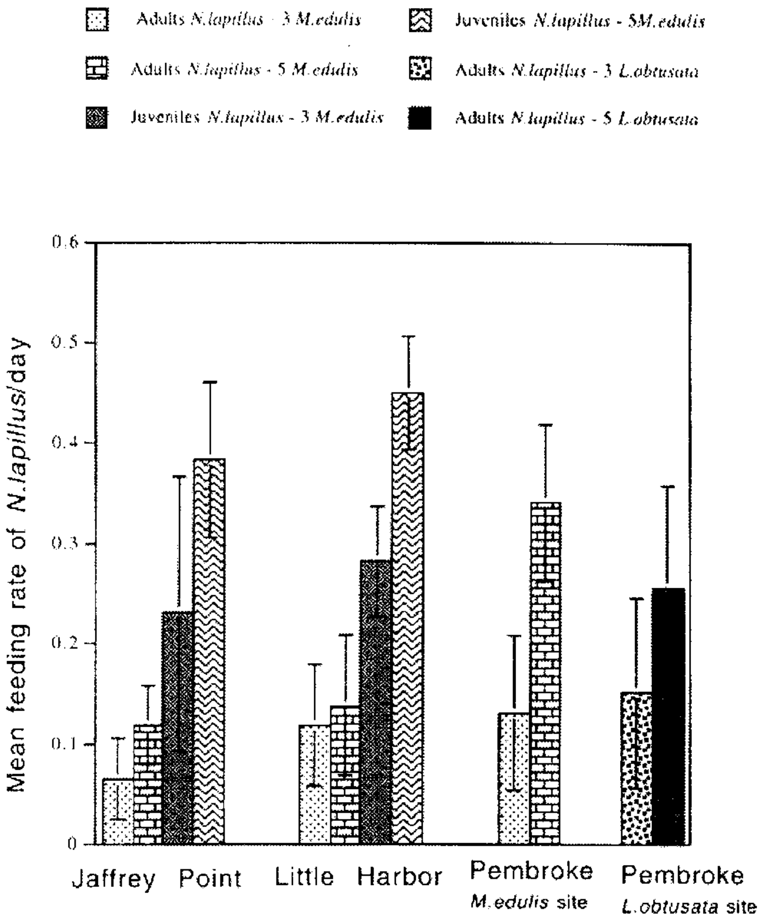

Figure 1 - Feeding rate of adults and juveniles of *Nucella lapillus* from Jaffrey Point, Little Harbor, NH and adults of *N. lapillus* from Pembroke, ME in two different treatments. Error bars = SD

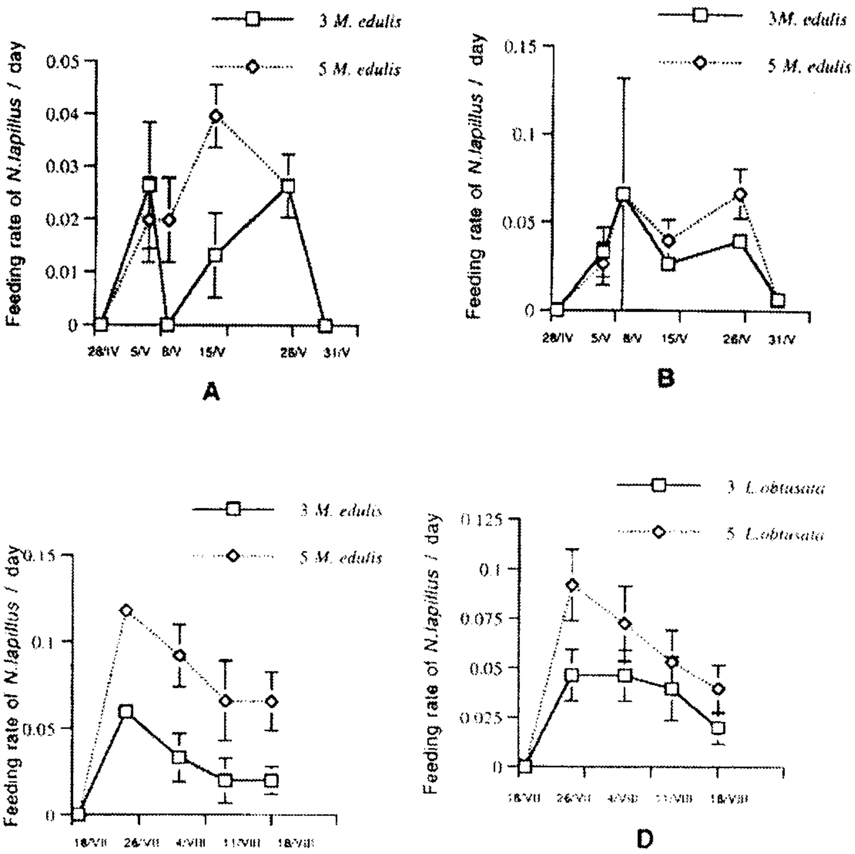

Figure 2 - Feeding rate of adults individuals of *Nucella lapillus* from Jaffrey Point (A) and Little Harbor, NH (B) in two different treatments, from 28 April to 31 May, 1995. Error bars = SD. Feeding rate of adults individuals of *Nucella lapillus* from two populations from Pembroke, ME (C and D) in two different treatments, from 18 July to 18 August, 1995. Error bars = SD

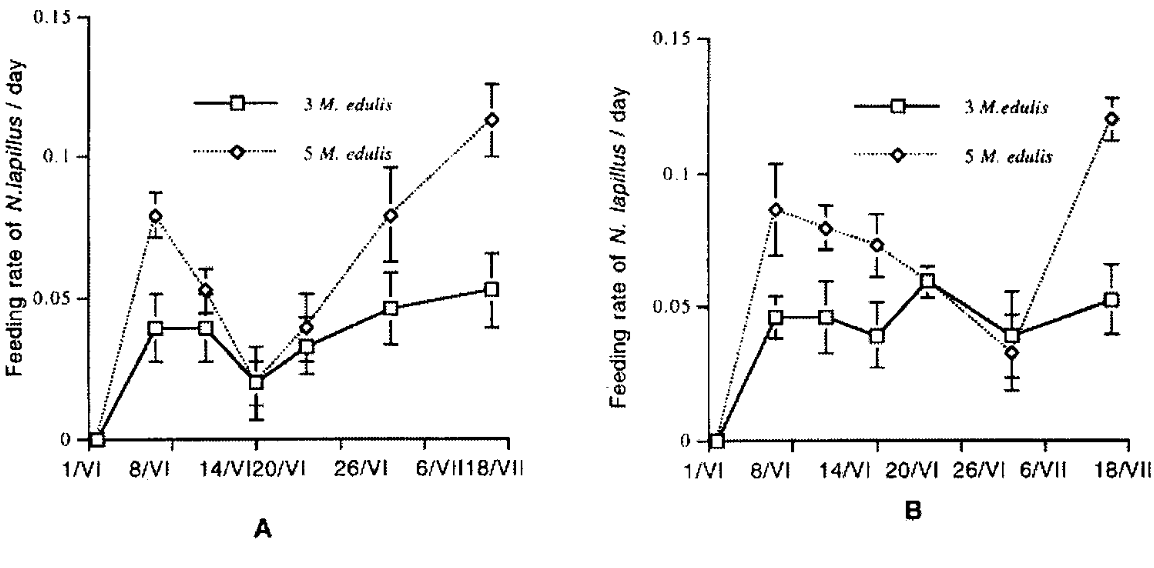

Figure 3 - Feeding rate of juveniles individuals of *Nucella lapillus* from Jaffrey Point (A), and Little Harbor, NH (B) in two different treatments, from 1 June to 18 July, 1995. Error bars = SD

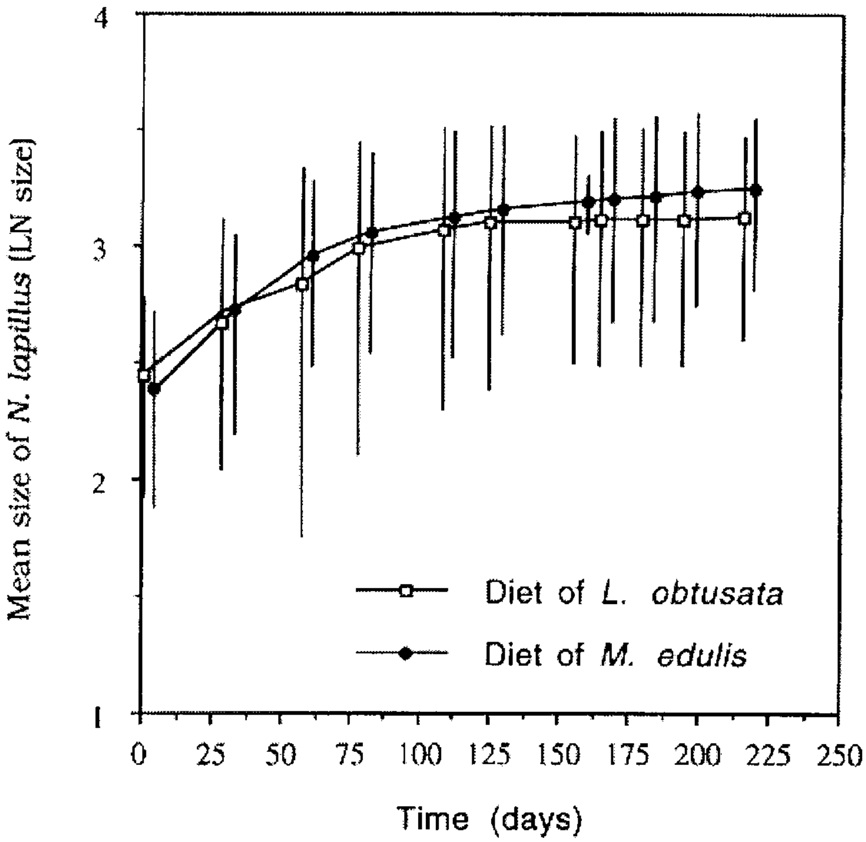

Figure 4 - Growth rate of *Nucella lapillus* from Pembroke, ME in a diet of *Littorina obtusata* and *Mytilus edulis* from 30 May 1995 to 02 January 1996. Data is transformed using a natural log. Bars represent 95% confidence intervals.

DISCUSSION

The positive correlation between feeding rate and prey density, observed in this study, may represent an adaptive response to a higher concentration of chemosensory or tactile cues of prey presence as *Nucella lapillus* is a nonvisual predator (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 adaptive response, as an increase in prey abundance can reduce predation effort related to capture, competition, and risks. Juveniles of *Thais haemastoma floridana* also showed an increase in predation rate at higher prey densities (Farias, 1997).

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 prey densities 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 satiation 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) (Matthews-Cascon, 2001). The differences in growth rates was probably related to the inherent food value of individual prey, as the number of prey eaten in each treatment was not significantly different.

The growth rate in Gastropoda is highest in the younger individuals and commonly declines rapidly with age (Wilbur, 1964; Wilbur & Owen, 1964; Kenny,1977). entaililng 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* showed a decline in the growth rate (Figure 4), 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 it was 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 *N.lapillus* on *M.edulis* and *L.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.

CONCLUSIONS

Adult and juvenile individuals of *N.lapillus* showed a higher feeding rate when more prey were available. This increase in feeding rate with prey density may represent a non-adaptive response to a concentration increase of chemosensory or tactile cues of prey presence, as *N.lapillus* is a nonvisual predator. 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 effort related to capture, competition, and risks.

Results obtained in the present study indicate that *M.edulis* has a greater potential "food value" than *L.obtusata* and the mean size of the individuals of *N.lapillus* measured in the field was higher in the population that prey on *M.edulis* than in the population that fed on *L. obtusata*.

REFERENCES

Annala, J. Foraging strategies and predation effects of *Asterias rubens* and *Nucella lapillus*. PhD Dissertation, University of New Hampshire, 1974.

Ballantine, W. J. A biologically-defined exposure scale for the comparative description of rocky shores. *Field Studies*, v. 3, p.1-19, 1961.

Brown, K. W. & Richardson, T. D. Foraging ecology of the southern oyster drill Thais haemastoma (Gray): constrains on prey choice. *J. Exp. Mar. Biol. Ecol.*, v.114, p.123-141, 1987.

Burrows, M. T. & Hughes, R. N. Natural foraging of the dogwhelk, *Nucella lapillus* (Linnaeus); the weather and whether to feed. *J. Moll. Stud.*, v. 55, p.285-295, 1989.

Burrows, M. T. & Hughes, R. N. Variation in growth and consumption among individuals and populations of dogwhelks *Nucella lapillus*: a link between foraging behaviour and fitness. *J. Anim. Ecol.*, v.59, p.723-742, 1990.

Colton, H. S. On some varieties of *Thais lapillus* in the Mount Desert Section, a study of individual ecology. *Proc. Acad. Nat. Sci. Phil.*, p.440-454, 1916.

Conover, R. J. & Lalli, C. M. Feeding and growth in *Clione limacina* (Philips), a pteropod mollusk. II. Assimilation, metabolism, and growth efficiency. *J. Exp. Mar. Biol. Ecol.*, v.16, p.131-154, 1974.

Crothers, J. H. On variation in *Nucella lapillus* (L.): shell shape in populations towards the Southern limit of its European range. *J. Moll. Stud.*, v. 43, p.181-188, 1977.

Darling, S.D. Observations on the growth of *Cypraea spadicea*. *The Veliger*, v.8, p.14-15, 1965.

Duarte, L. F. L. Um estudo de interação predador-presa em costões rochosos marinhos da Estação Ecológica de Juréia-Itains, São Paulo. *Anais da 3 Reunião Especial da SBPC: Ecossistemas Costeiros*, UFSC., p. 67-68.

Edwards, D. G. & Huebner, J. D. Feeding and growth rates of *Polinices duplicatus* preying on *Mya arenaria* at Barnstable Harbor, Massachusetts. *Ecology*, v.5, p.89-92, 1977.

Etter, R. J. Physiological stress and color polymorphism in the intertidal snail *Nucella lapillus*. *Evolution*, v.42, p.660-680, 1988.

Farias, M. F. Estudo do comportamento alimentar de juvenis de *Thais haemastoma floridana* (Conrad, 1837) (Mollusca: Gastropoda: Thaididae) em condições de laboratório. Monografia, Ciências Biológicas, Universidade Federal do Ceará, 20 p., 1997.

Feare, C. J. The reproductive cycle of the dogwhelk (*Nucella lapillus*). *Proc. Malacol. Soc. London*, v.39, p.125-137, 1970.

Frank, P. W. The biodemography of an intertidal snail population. *Ecology*, v.46, p.831-844, 1965.

Fretter, V. & Graham, A. *British prosobranch mollusks*. The Ray Society, 820 p., London, 1994.

Hughes, R. N. Optimal foraging theory in the marine context. *Ann. Rev. Ocean. Mar. Biol.*, v.18, p. 423-481, 1980.

Hughes, R. N. *A functional biology of marine gastropods*. The Johns Hopkins University Press, 245 p., Baltimore, Maryland, 1986.

Hyman, H. L. *The invertebrates. Vol.. VI – Mollusca I. Aplacophora, Polyplacophora, Monoplacophora, Gastropoda. The coelomate bilateria*. McGraw-Hill Book Company, 792 p., New York, 1967.

Joosse, J. & Geraerts, W. P. M. *Endocrinology. In, The Mollusca. Vol.4 Physiology. Part. 1*, edited by A. S. M. Saleuddin e K.L. Wilbur, Academic Press, p. 317-406, New York, 1983.

Katoh, M. Life history of the golden ring cowry *Cypraea annulus* (Mollusca: Gastropoda) on Okinawa Island, Japan. *Mar.Biol.*, v.101, p.227233, 1989.

Kenny, R. Growth studies of the tropical intertidal limpet *Acmaea antilarum*. *Mar. Biol.*, v. 39, p. 161-170, 1977.

Kirby, R. R. & Bayne, B. L. Physiological variation in the dogwhelk *Nucella lapillus*, L. either side of a cline in allozyme and karyotype frequencies. *Biol. J. Linn. Soc.*, v. 53, p. 277-290, 1994.

Kohn, A. J. Chemoreception in gastropod mollusks. *Amer. Zool.*, v. 1, p. 291-308, 1961.

Krebs, J. Optimal foraging: theory and experiment. *Nature*, v. 268, p. 583-584, 1977.

Laxton, J. H. Shell growth in some New Zealand Cymatiidae (Gastropoda: Prosobranchia). . *J. Exp. Mar. Biol. Ecol.*, v. 4, p. 250-260, 1970.

Lull, W. W. Predation by *Thais lapillus* on *Littorina obtusata*. M.Sc. Thesis, University of New Hampshire, 70 p., 1979.

Mathieson, A. C.; Hehre, E.J. & Reynolds, N. B. Investigations of New England marine algae I: A floristic and descriptive ecological study of the marine algae at Jaffrey Point, New Hampshire, U.S.A. *Bot. Mar.*, v. XXIV, p. 521-532, 1981.

Matthews-Cascon, H. Prey preference and recognition by *Nucella lapillus* (Linnaeus, 1758) (Mollusca: Gastropoda). *Arq. Ciên. Mar.*, v. 34, p. 87-97, 2001.

Menge, B. A. Organization of the New England rocky intertidal community: role of predation, competition, and environmental heterogeneity. *Ecol. Monogr.*, v. 46, p. 355-393, 1976.

Moore, H. B. The biology of *Purpura lapillus*. I. Shell variation in relation to environment. *J. Mar. Biol. Ass. UK.*, v. 21, p. 61-89, 1936.

Moore, H. B. The biology of *Purpura lapillus*. Part III. Life history and relation to environmental factors. . *J. Mar. Biol. Ass. UK.*, v. 23, p. 67-74, 1938.

Moran, M. J.; Fairweather, P. G. & Underwood, A.J. Growth and mortality of the predatory intertidal whelk Morula marginalba Blainville (Muricidae): the effects of different species of prey. *J. Exp. Mar. Biol. Ecol.*, v.75, p.1-17,1984.

Morse, D. H. *Behavioral mechanisms in ecology*. Harvard University Press, viii + 383 p, Cambridge, 1980.

Murdoch, W.W. The development response of predators to changes in prey density. *Ecology*, v. 52, p. 132-137, 1971

Palmer, A. R. Growth in marine gastropods: a non-destructive technique for independently measuring shell and body weight. *Malacologia*, v. 23, p. 63-73, 1982.

Palmer, A. R. Growth rate as a measure of food value in thaidid gastropods: assumptions and implications for prey morphology and distribution. *J. Exp. Mar. Biol. Ecol.*,v. 73, p. 95-124, 1983.

Palmer, A. R. Prey selection by thaidid gastropods: some observational and experimental field tests of foraging models. *Oecologia*, v. 62, p. 162-172, 1984.

Palmer, A. R. Effect of crab effluent and scent of damage conspecifics on feeding, growth, and Shell morphology of the Atlantic dogwhelk *Nucella lapillus* (L.). *Hydrobiologia*, v. 193, p. 155-182, 1990.

Randall, H. A. A study of the growth and other aspects of the biology of the West Indian topshell, *Cittarium pica* (Linnaeus). *Bull. Mar. Sci. Gulf. Caribbean*, v. 14, p. 424-443, 1964.

Spight, T.M. Sizes of populations of a marine snail. *Ecology*, v.55, p. 712-729, 1974.

Stephens, D.W. & Krebs, J.R. *Foraging Theory*. Princeton University Press, 247 p., Princeton, 1986.

Wilbur, K.M. Shell formation and regeneration. In, *Physiology of Mollusca*, edited by K.M. Wilbur e C.M. Yonge. Academic Press, New York, p. 243-282, 1964.

Wilbur, K.M. & Owen, G. Growth. In, *Physiology of Mollusca*, edited by K.M. Wilbur e C.M. Yonge. Academic Press, New York, p.211-242, 1964.

Wilbur, K.M. & Saleuddin, A.S.M. Shell formation. In, *The Mollusca, vol. 4 Physiology*. Part.1, edited by A.S.M. Saleuddin e K.M. Wilbur, Academic Press, New York, p. 235-287, 1983.

Yamaguchi, M. Shell growth and mortality rates in the coral reef gastropod *Cerithium nodulosum* in Pago Bay, Mariana Islands. *Mar. Biol.* v.44, p. 249-263, 1977.

Zischke, J.A.; Watabe, N. & Wilbur, K.M. Studies on shell formation: measurement of growth in the gastropod *Ampularius glaucus*. Malacologia, v. 10, p. 423-439, 1970.