

## Prey selection by inexperienced predators: do early juvenile snails maximize net energy gains on their first attack?

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### Abstract

Through encounters with prey, a predator may learn to become more selective and thus forage more efficiently. This is the case for several muricid gastropods. When searching for their first prey, however, early juveniles have no such foraging experience. Prey species and prey size preferences of inexperienced *Nucella emarginata* (Deshayes) hatchlings from Barkley Sound, British Columbia, Canada, were therefore examined to determine if selective feeding occurs in the absence of foraging experience and, if so, whether the preferences are consistent with the energy maximization hypothesis of optimal foraging theory. When given a choice between 5 prey species (small *Mytilus* spp., *Balanus glandula* (Darwin), *Chthamalus dalli* (Pillsbury), *Pollicipes polymerus* (Sowerby) and *Lasaea* spp.), 80% of the hatchlings attacked *Mytilus* spp. on their first attack. When offered 5 size classes (1, 2, 3, 4 and 5 mm shell length) of *Mytilus* spp.,  $\approx 73\%$  of the hatchlings attacked 1-mm or 2-mm size classes. Hatchlings were, in fact, more selective than late juveniles and adults. Hence, strong prey species and size preferences can exist without prior foraging experience even in species which use such experience later in life to make foraging decisions. But hatchlings feeding on *Mytilus* spp. for 25 days did not grow faster than hatchlings feeding on *Balanus glandula* or *Chthamalus dalli*, and there was no difference in energy content between *Mytilus* spp. and *Chthamalus dalli*. Thus, the strong preference for small *Mytilus* spp. can not be explained by considerations of energy gain. In the field, small *Mytilus* spp. are mostly located in microhabitats which provide hatchlings with substantial protection from mortality factors. The preference for small *Mytilus* spp. should keep the young snails within protective microhabitats once these sites have been reached, and might be an adaptation to help the hatchlings locate these havens from a distance, in an otherwise highly dangerous environment.

**Keywords:** Energy maximization; Foraging; Growth; Microhabitats; Predation

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## 1. Introduction

Foraging experience can be an important basis for decisions that influence searching and handling efficiency as well as food preferences (Wood, 1968; Hughes, 1979; Derby and Atema, 1981; Bayliss, 1982; Johnson, 1991). Through a series of encounters with prey, individuals may learn to become more efficient at locating prey, feed on fewer species or on a narrower range of sizes of prey and abandon less efficient methods of attack (Hughes, 1980; Hughes and Dunkin, 1984a; Johnson, 1991). This implies that individuals with less experience are less selective. In reality, it is not known whether organisms that make foraging decisions based on experience require such experience to be selective.

The advantages of using intertidal snails for studying foraging behaviour are well documented (Palmer, 1984, 1990; Hughes and Burrows, 1991). *Nucella emarginata* (Deshayes) (northern: Palmer et al., 1990), an intertidal predatory gastropod, is particularly suitable for studying the selectivity of experienced and inexperienced individuals. Prior feeding experience does influence decisions regarding selection of prey species and size in late juvenile and adult *N. emarginata* (Palmer, 1984) and in other thaidine gastropods (Menge, 1974; Palmer, 1984; Hughes and Dunkin, 1984b). However, when young *N. emarginata* hatch, after having completed larval development within a benthic egg capsule, they have no direct information on the distribution, abundance, or value of nearby prey. Newly hatched muricids may obtain some information through chemosensory detection of prey (Williams et al., 1983), but the usefulness of this information is unclear. Chemotactic responses to prey species may in fact be suppressed by exposure to their odours during development (Rittschof et al., 1984). In any case, prey odours would not provide detailed knowledge of the abundance and distribution of nearby prey. In addition, snails emerging from their egg capsule have no experience pertaining to the costs and benefits of each prey type.

When newly hatched *N. emarginata* search for food items for the first time, they must decide whether to attack or reject each item encountered without the benefit of experience from previous encounters. As a result, young snails might be expected to be less selective than older individuals. However, selecting prey that promote the fastest growth could be beneficial to hatchlings because this might shorten the period during which they are in the smallest, most vulnerable sizes (Vermeij, 1972, 1978, 1987; Werner and Gilliam, 1984; Gosselin and Chia, 1995a). This is important because newly hatched *N. emarginata* are extremely vulnerable to predators and physical stresses (Gosselin and Chia, 1995a) and cohorts of intertidal thaidine gastropods suffer considerable mortality early in life (Feare, 1970; Spight, 1975). Strong prey preferences established at the onset of independent benthic life might also enhance survival through the early juvenile period if newly hatched individuals prefer prey that are mainly located in protective microhabitats.

The objectives of this study were therefore to: (1) examine prey species and prey size selection by newly hatched *N. emarginata* when attacking their first prey to determine if inexperienced hatchlings are less selective than older, experienced individuals, and, thus, if feeding experience is the main basis for selective foraging; (2) determine if hatchlings prefer prey that promote the fastest growth, consistent with the energy maximization

hypothesis of optimal foraging theory (Pyke et al., 1977; Hughes, 1980; Palmer, 1983); and (3) compare prey preferences (this study) with the distribution of prey in the field (Gosselin and Chia, 1995b) to determine if newly hatched *N. emarginata* prefer prey that are located in microhabitats providing the best protection.

## 2. Materials and methods

### 2.1. Study site and organism

The experiments described herein were carried out at the Bamfield Marine Station, British Columbia, Canada, from December 1991 to September 1992. All organisms were collected at nearby sites in Barkley Sound. *N. emarginata* hatchlings used in the following experiments had been spawned in the field and had undergone complete larval development in their natural environment. Ripe capsules (unplugged capsules containing metamorphosed individuals that had not yet emerged) were collected in the field and placed in cages in flowing sea water in the laboratory. Hatchlings that emerged in the laboratory during the first 24 h after collecting the capsules were placed in a separate cage until later use; the age of the hatchlings used in each experiment was therefore known with an accuracy of 24 h (time of emergence is considered  $t = 0$ ). Because most *N. emarginata* do not feed during the first 3–10 days after emerging from their egg capsule (Gosselin and Chia, 1994), newly hatched individuals (0.9–1.8 mm shell length) were placed in otherwise empty cages in flowing seawater for 15 to 18 days before being used in the following experiments. These hatchlings therefore had no contact with prey prior to experimentation. Each snail was used only once in this study.

### 2.2. Prey preferences

#### 2.2.1. Prey species selection

To determine if feeding experience is a prerequisite for selective feeding by *N. emarginata*, inexperienced *N. emarginata* hatchlings from Kirby Point (48°50'85" N, 125°12'40" W) were enclosed with 5 prey species (*Mytilus* spp., *Lasaea* spp., *Balanus glandula*, *Chthamalus dalli* and *Pollicipes polymerus*) and the first item to be attacked was identified. Of the 6 species that can be used as prey by newly hatched *N. emarginata* (Gosselin and Chia, 1994) only *Musculus taylori* (Dall) was not offered, as this species was absent or rare at most field sites (Gosselin and Chia, 1995b) and could not be found in sufficient quantities at the time of this experiment. Very small cages (modified centrifuge micro test tubes, 11 mm diam.  $\times$  14 mm long, provided with 610  $\mu$ m mesh screening), hereafter referred to as micro cages, received 1 hatchling and the following 5 prey items: one small *Mytilus* spp. (2–3 mm shell length; included *M. trossulus* (Gould) and *M. californianus* (Conrad) which could not be distinguished at this size), one *Balanus glandula* (2–4 mm shell diameter, rostro-carinal axis), one *Chthamalus dalli* (2–4 mm shell diameter), one *Lasaea* spp. (2–3 mm shell length), and one *Pollicipes polymerus* (2–3 mm shell diameter, measured at the widest area of the scutum). Individual *Balanus glandula* and *Chthamalus dalli* were obtained by breaking

off small pieces of mussel and barnacle shells to which they were attached. *Pollicipes polymerus* were gently detached from the bases of adults and placed in flowing seawater for 48 h; individuals surviving this period were used in the present experiment. The cages containing predators and prey then were placed in flowing seawater for 3.75 days, after which each prey item was examined under a dissecting microscope for evidence of drilling. In most cases hatchlings only had time to attack one prey. All attacks, complete and incomplete, were recorded.

### 2.2.2. Prey size selection

Based on the results of the prey species selection experiment, hatchlings obtained from Dixon Island (48°51'15" N, 125°06'90" W) were offered a range of sizes of small *Mytilus* spp., the preferred species, to determine if inexperienced hatchlings also had prey size preferences. One hatchling and 5 mussels, of shell length size classes 1 (1.04–1.25 mm), 2 (1.8–2.2 mm), 3 (2.8–3.2 mm), 4 (3.8–4.2 mm) and 5 (4.8–5.2 mm) were placed in micro cages for 5 days. All mussels were then examined under a dissecting microscope for evidence that the shell had been drilled.

## 2.3. Significance of prey preferences

If foraging decisions made by inexperienced hatchlings are consistent with the energy maximization premise, prey that provide the greatest energy return should be preferred. To determine if this is the case, growth of hatchlings and prey energy content were examined.

### 2.3.1. Hatchling growth vs. prey species

The net energetic benefit of each prey species to hatchlings was examined by providing hatchlings with a single prey species for 25 days and measuring their growth over this period. Unfed hatchlings 16–19 days old were individually marked with nail polish colour codes using the method described by Gosselin (1993), and measured using the ocular micrometer of a dissecting microscope ( $\pm 0.0392$  mm). Marked hatchlings were then placed in cages (modified plastic vials, 39 mm diam.  $\times$  62 mm long, hereafter referred to as vial cages), 3 cages for each prey species, containing 6 or 7 hatchlings ( $n = 20$  hatchlings per prey treatment). Hatchlings were offered either *Mytilus* spp. (1–10 mm shell length), *Balanus glandula* (2–8 mm shell diameter), *Chthamalus dalli* (1.5–6 mm shell diameter), *Lasaea* spp. (1.5–4.5 mm shell length) or *Pollicipes polymerus* (2–10 mm shell diameter). Each cage contained 70–120 prey items. To determine if a varied diet can produce faster growth, an additional set of 3 vial cages each containing 24 items of each prey species was also included in the experiment. The cages were then placed in 3 aerated 40-l aquaria; each aquaria received 1 cage from each prey treatment (complete block design, 3 aquaria with 6–7 replicate snails per aquaria). The aquaria were large relative to the few hatchlings and small prey items they contained and the prey and hatchlings were not tightly packed within any of the cages. After 25 days all

classes as follows: 1.0–1.9  $\mu\text{l}$ , 3 individuals; 2.0–2.9  $\mu\text{l}$ , 2 individuals; 3.0–3.9  $\mu\text{l}$ , 1 individual. Volume and energy content measurements were then used to calculate energy density ( $\text{J}/\mu\text{l}$  body volume).

Some reduction in accuracy will have resulted from the use of total body volume (including the shell) rather than internal body cavity volume (volume within the prey's shell) to calculate energy density. Also, the use of the entire animal, including the shell, in the dichromate oxidation analysis can affect the results. Although the shell contains relatively little organic material (<5% by weight in mollusc shells, Lowenstam and Weiner, 1989), it becomes pulverised during the procedure and when suspended may interfere with spectrophotometer readings. We found, however, that the shell material sedimented out of the solution within 24 h; readings from the glucose standards did not change over this period. Consequently, spectrophotometer readings were taken 24 h after oxidation of the samples.

### 3. Results

#### 3.1. Prey preferences

##### 3.1.1. Prey species selection

When attacking their first prey, *Nucella emarginata* hatchlings did not attack randomly: observed attack frequencies were significantly different from an even distribution of attacks among species (single attacks, Goodness of fit test:  $G_{\text{adj}} = 34.327$ ,  $P < 0.001$ ,  $df = 4$ ;  $G$  value adjusted using Williams' correction, Sokal and Rohlf, 1981). *Mytilus* spp. was attacked much more often than any other species (Fig. 1). Of the 20 hatchlings that attacked only 1 prey item, 80% attacked *Mytilus* spp. In each case where hatchlings had attacked 2 ( $n = 2$ ) or 3 ( $n = 1$ ) items, *Mytilus* spp. was one of the attacked prey.

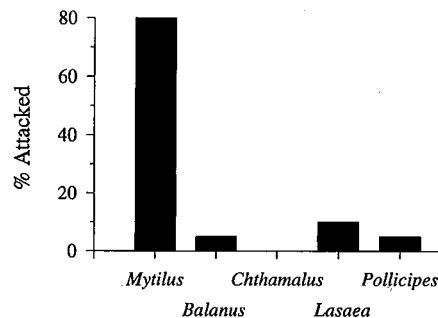


Fig. 1. Prey species attacked by hatchling *Nucella emarginata* encountering prey for the first time. Twenty replicate micro cages each received 1 hatchling and 1 item of each prey species for 3.75 days. Each hatchling attacked no more than 1 prey item during this experiment. Values shown are the percentage of attacks on each of 5 prey species. Attack frequencies were significantly different from a 1:1:1:1:1 ratio (see text).

hatchlings were remeasured. Hatchlings consumed less than 75% of the prey items during the 25-day period so that prey availability was not believed to be a limiting factor.

No growth data were obtained from snails feeding on *P. polymerus*. Most of the large *P. polymerus* died and were in an advanced state of decomposition at the end of the 25-day period. Eighteen of the 20 hatchlings in this treatment also died. Because *P. polymerus* species is typically found at sites exposed to intense wave action or high currents, it presumably could not tolerate the comparatively low flow conditions existing in the cages. In each of the other prey treatments, a maximum of 3 out of 20 hatchlings died during the same period.

### 2.3.2. Energy content of prey

To compare energy density among prey size classes and species, the volume and energy content of 3 size classes of *Mytilus* spp., *Lasaea* spp., *Chthamalus dalli* and *Balanus glandula* were measured in September 1992. The body volume of individual prey items was determined using water displacement measurements. For the 2 barnacle species (*B. glandula* and *Chthamalus dalli*), individuals were obtained by gently detaching the base of their shell from the rock surface using the blade of a scalpel. If flesh remained attached to the rock, the individual was not used. These results were then used to calculate a regression equation between body volume and shell length (*Mytilus* spp. and *Lasaea* spp.) or diameter (*Chthamalus dalli* and *Balanus glandula*) (Table 1). For *Mytilus* spp. and *Lasaea* spp., these equations were then used to determine the ranges in shell length corresponding to the 1.0–1.9  $\mu\text{l}$ , 2.0–2.9  $\mu\text{l}$  and 3.0–3.9  $\mu\text{l}$  volume classes. For *Chthamalus dalli* and *Balanus glandula*, however, the correlation between diameter and body volume was not as strong (Table 1); volume measurements were therefore carried out for each specimen included in the energy content analysis.

New samples of prey were then collected from the field, individuals of appropriate sizes were selected, and, within 24 h of collection, their energy content was determined by dichromate oxidation against a glucose standard using the method described by McEdward and Carson (1987). This method quantifies total organic carbon; organic carbon values were converted to total energy using the formula:  $1 \mu\text{g C} = 3.90 \times 10^{-2} \text{ J}$ , based on constants in Parsons et al. (1984). Because the amount of organic material present in the smallest individuals was close to the limits of detection of the method, more than 1 individual were placed in each replicate test tube for the smallest size

Table 1

Relationship between body volume and linear size measurements of 4 species used as prey by *Nucella emarginata* hatchlings.

Prey species	Regression equation*	$R^2$	$n$	Size range measured	Collection site
<i>Mytilus</i> spp.	$\text{Vol} = 0.095 \times \text{SL}^3$	0.974	24	1.52–5.92 mm SL	Wizard Islet
<i>Lasaea</i> spp.	$\text{Vol} = 0.175 \times \text{SL}^3$	0.960	24	0.96–3.12 mm SL	Wizard Islet
<i>Chthamalus dalli</i>	$\text{Vol} = 0.056 \times \text{SD}^3$	0.783	24	1.58–3.36 mm SD	Ross Islets
<i>Balanus glandula</i>	$\text{Vol} = 0.096 \times \text{SD}^3$	0.919	23	2.56–7.60 mm SD	Ross Islets

Regression equations were calculated using 0 as intercept.

\*Vol, body volume ( $\mu\text{l}$ ); SL, shell length (mm); SD, shell diameter, measured along rostro-carinal axis (mm).

### 3.1.2. Prey size selection

If inexperienced hatchlings attacked *Mytilus* spp. as they encountered them, the distribution of attacks among size classes should reflect some measurement of mussel body size, the likelihood of encounter increasing with size. An expected attack frequency was calculated, which assumed no size selection by the hatchlings, using mussel body volume as an indicator of the likelihood of encounter. Although a two-dimensional measurement of area occupied by the mussel might seem more appropriate, the actual area occupied depends on the position of the mussel relative to the substratum. The volume occupied by a mussel was therefore used as a simple, although less conservative, way of approximating relative likelihood of encounter. Mussel volume for each size class was calculated using the regression equation in Table 1.

The expected and actual attack frequencies showed contrasting patterns (Fig. 2). Of the 22 hatchlings that attacked a single mussel during the 5-day period, 72.7% of these attacked 1- or 2-mm prey (single attacks, Fig. 2). Attacks on 4- and 5-mm mussels totalled only 9.1%. A similar pattern was obtained when results from the remaining 13 hatchlings that attacked 2 prey were included (all attacks, Fig. 2). Single-attack frequencies were significantly different from expected-attack frequencies using body volume as an indicator of encounter likelihood (Goodness of fit test:  $G_{adj}=97.871$ ,  $P<0.001$ ,  $df=4$ ). Although 5-mm mussels occupied 125 times more space than 1-mm mussels, 1-mm mussels were attacked 8 times more often.

### 3.2. Significance of prey preferences

#### 3.2.1. Hatchling growth vs. prey species

Hatchling growth differed significantly among prey species treatments (complete block ANOVA, the aquaria used as blocks:  $F=3.36$ ,  $P=0.015$ ,  $n=89$ ). Hatchlings

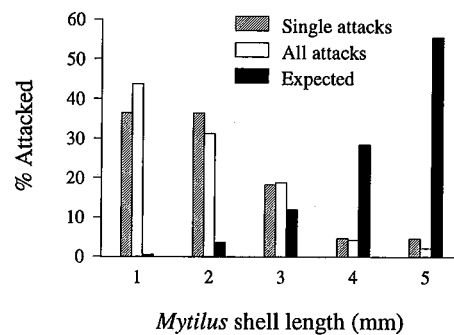


Fig. 2. Attacks on 5 *Mytilus* spp. size classes by hatchling *Nucella emarginata* encountering prey for the first time. Hatchlings were individually placed in micro cages with 1 mussel of each size class for 5 days. Values shown are the percentage of attacks on each of 5 size classes by hatchlings that attacked only 1 prey (single attacks,  $n=20$ ) or by hatchlings that attacked either 1 or 2 prey items (all attacks,  $n=35$ ). Also shown are the attack frequencies expected if mussels were attacked as they were encountered, using mussel body volume as an estimator of likelihood of encounter.

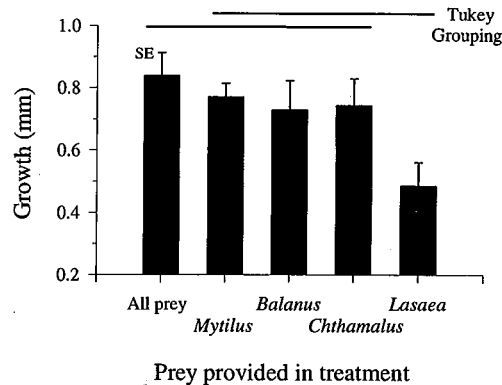


Fig. 3. Growth of *Nucella emarginata* hatchlings, provided with 5 prey species (all prey treatment) or with single prey species, over a period of 25 days. The lines along the top of the figure indicate mean values that were not significantly different (Tukey grouping,  $\alpha=0.05$ ,  $n=16$  to 19 hatchlings per treatment).

feeding on *Lasaea* spp. grew less during the 25-day period than did hatchlings in the all-prey treatment (Fig. 3). No significant difference in growth was detected between hatchlings provided with *Mytilus* spp., *Balanus glandula* or *Chthamalus dalli*.

### 3.2.2. Energy content of prey

Within each prey species the amount of energy per unit body volume ( $J/\mu l$ ; Fig. 4) did not differ significantly between size classes (ANOVA: *Mytilus* spp.:  $F=0.21$ ,  $P=0.816$ ,  $n=21$ ; *Chthamalus dalli*:  $F=1.62$ ,  $P=0.226$ ,  $n=21$ ; *Lasaea* spp.:  $F=0.91$ ,  $P=0.358$ ,  $n=14$ ). Data from different size classes were therefore pooled for among-

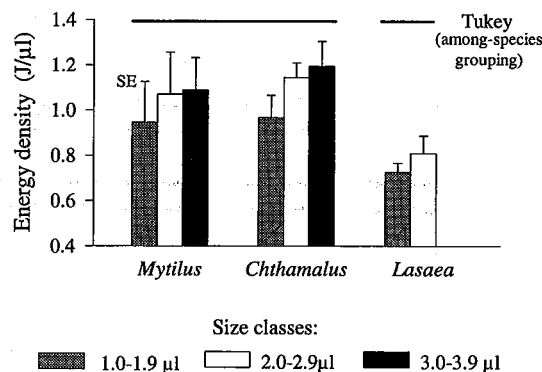


Fig. 4. Energy density, in  $J \cdot \mu l^{-1}$ , of 3 size classes of *Mytilus* spp., *Chthamalus dalli* and *Lasaea* spp. ( $n=7$  for each value shown). Few 3.0–3.9  $\mu l$  *Lasaea* spp. were obtained at the time of the study, and thus no results are available for *Lasaea* spp. in this size class. Energy density of size classes of a same species were not significantly different (see text). The lines along the top of the figure link species values that were not significantly different (Tukey grouping,  $\alpha=0.05$ ,  $n=14$  (*Lasaea* spp.) or 21 per treatment).



species comparisons. Energy densities were significantly different between species (ANOVA,  $F=4.88$ ,  $P=0.011$ ), being higher in *Mytilus* spp. ( $1.034 \pm 0.434$  J/ $\mu$ l) and *Chthamalus dalli* ( $1.101 \pm 0.255$  J/ $\mu$ l) than in *Lasaea* spp. ( $0.767 \pm 0.161$  J/ $\mu$ l). Energy densities of *Mytilus* spp. and *Chthamalus dalli* were not significantly different. Inaccurate results were obtained when analysing the energy content of *Balanus glandula* such that these results could not be used.

#### 4. Discussion

##### 4.1. Prey selection by inexperienced individuals

When attacking their first prey item, hatchling *Nucella emarginata* strongly preferred *Mytilus* spp. over any of the other 4 species offered. In addition, the inexperienced hatchlings preferred 1–2 mm mussels, the smallest available size classes. The largest *Mytilus* spp. size class offered (5-mm shell length) was well within the range of sizes that hatchlings can successfully attack, since mussels as large as 10 mm have been successfully drilled through by hatchlings in the laboratory, and 5-mm mussels were readily consumed when these alone were offered as prey (Gosselin, personal observation). Also, hatchling *Nucella emarginata* can feed and grow on any of the species offered in this study (Fig. 3), and they do feed at least occasionally on these species in the field (Gosselin and Chia, 1994). In the laboratory, *N. emarginata* can be reared for several generations on a diet of barnacles (Palmer, 1985). Nevertheless, the strong preference for small *Mytilus* spp. was repeatedly observed in different feeding experiments using hatchlings from other sites in Barkley Sound (Gosselin and Chia, 1994; Gosselin, personal observation).

Clearly, strong prey species and size preferences can be established without prior foraging experience even in species, such as *Nucella emarginata*, which use this experience later in life to make foraging decisions. In fact, newly hatched *N. emarginata* were considerably more selective than has been reported for late juvenile and adult *N. emarginata* (Palmer, 1984) or for late juveniles and adults of other thaidine gastropods (Hughes and Dunkin, 1984a; Palmer, 1984; West, 1986; Brown and Richardson, 1987; Gosselin and Bourget, 1989).

During the first 4 weeks after hatching, *N. lapillus*, an Atlantic coast species, can feed on a variety of prey species (Largen, 1967), but small mussels (sizes not specified) form the major part of their diet (Feare, 1970). This suggests that the preferences described herein for newly hatched *N. emarginata* may be of broader occurrence among intertidal thaidine gastropods.

It may seem surprising that food preferences can be highest before foraging experience is acquired in an animal that is known to use such experience later in life to improve foraging efficiency. However, the range of prey species and sizes most preferred by an animal might be independent of experience early in life if the adaptive reason for selecting prey changes during ontogeny, as is discussed in Section 4.3.

#### 4.2. Prey preferences and energy maximization

An important assumption of the energy maximization hypothesis is that the growth potential of a food type is a good indicator of its fitness value to the consumer (Charnov, 1976; Hughes, 1979; Palmer, 1983). Growth rate has indeed been shown to be related to fitness attributes in *N. emarginata* (Palmer, 1983). In this study, however, the preferred prey, *Mytilus* spp., did not promote faster growth in hatchlings than did *Balanus glandula* or *Chthamalus dalli*. Prey energy density measurements, which allow comparisons of energy content per unit body size, were consistent with growth measurements: no significant difference in energy density was found between *Mytilus* spp. and *Chthamalus dalli*. The lack of difference in growth and in energy density suggest that handling costs for each prey species were also equivalent or that the maximum net amount of energy that can be assimilated per unit time was reached when feeding on either of these prey species.

Previous studies have identified 3 possible patterns of prey selection (not necessarily mutually exclusive): non-selective, frequency dependent, and energy maximization (Palmer, 1984, and references therein). These patterns are based on differences in the importance of ingestive conditioning (Wood, 1968; Morgan, 1972) or of energetic considerations on choice of food type. Physiological constraints and risk of predation, competition, or physiological stress can also influence prey preferences (e.g., by favouring prey that require less handling time), but these generally act to reduce selectiveness and increase the use of prey providing inferior energetic returns as a compromise between maximizing net energy return and minimizing risk (Menge, 1974; Lima and Dill, 1990; Burrows and Hughes, 1991a,b). The present results on hatchling growth and energy content of prey indicate that *Mytilus* spp., *Balanus glandula*, and *Chthamalus dalli* are of similar energetic value to the hatchlings; if hatchlings select prey based on considerations of energy gain, they should show no preference among these 3 species. This was not the case. In fact, their strong preference for *Mytilus* spp. over *Balanus glandula* and *Chthamalus dalli* did not comply with either of the above 3 patterns: feeding was highly selective but was not a result of ingestive conditioning (these hatchlings had never encountered prey) and hatchlings did not discriminate between prey based on ranking of energy return, with the exception of *Lasaea* spp. Clearly, other factors not yet considered can also produce strong food preferences.

Hatchlings did not grow faster when provided with a variety of prey species (Fig. 3), which is consistent with the hypothesis that *Nucella emarginata* have little or no need to complement their nutrient uptake by feeding on more than one species (Palmer, 1983).

It was not possible to determine whether mussel size preferences conformed with the energy maximization hypothesis. The growth potential of different sizes of *Mytilus* spp. were not examined because the preferred mussel size undoubtedly changes as the snail grows, as is the case among larger juvenile and adult *Nucella lapillus* (Hughes and Dunkin, 1984a; Harris, 1988).

#### 4.3. Prey used as indicators of protective microhabitats

Newly hatched *N. emarginata* can feed on at least 6 species of invertebrates that co-occur with the hatchlings in the field (Gosselin and Chia, 1994). Of these, small

*Mytilus* spp. (<5 mm shell length) and *Lasaea* spp. are the only ones to be abundant and almost exclusively found within the same microhabitats as *Nucella emarginata* hatchlings. *Lasaea* spp., however, are most abundant among dense assemblages of *Semibalanus cariosus*, the least effective shelter of the 3 hatchling microhabitats, while small *Mytilus* spp. are most abundant in tufts of *Cladophora columbiana*, the most effective shelter (Gosselin and Chia, 1995b). The strong preference for very small *Mytilus* spp. might, therefore, keep the young snails within protective microhabitats once these sites have been reached. If hatchlings are capable of locating prey from a distance, small *Mytilus* spp. could even be used as reliable cues to help the hatchlings locate these havens in an otherwise highly dangerous environment. Predatory marine gastropods are known to locate prey by following prey odours (Kohn, 1961; Wood, 1968; Morgan, 1972; Palmer, 1984), and even newly hatched muricid snails respond to prey odours (*Urosalpinx cinerea*, Williams et al., 1983; Brown and Rittschof, 1984). Small *Mytilus* spp. can reach densities of 2056 individuals/100 cm<sup>2</sup> within protective microhabitats, but are virtually absent on open surfaces (Gosselin and Chia, 1995b), and, therefore, might constitute effective cues for locating those refuges. If not, they should at least contribute to keeping the hatchlings therein once they have entered a refuge.

Early juvenile *Mytilus* spp. probably use such refuges for the same reasons as hatchlings (i.e., to avoid desiccation, predators and dislodgement by waves; also see Petersen, 1984). For small *Mytilus* spp., the risk of being killed by hatchlings is probably small relative to the risk of mortality on open surfaces since early juvenile mussels are probably vulnerable to the same factors as hatchlings, mainly desiccation and predation by decapod predators.

Since hatchlings may not survive 1 full tidal cycle if not located in protective microhabitats (Gosselin and Chia, 1995b), this intense selective pressure could explain why prey species and size preferences are so strong at the onset of independent benthic life. For example, if a hatchling feeds on the less-preferred barnacles, which are mainly located on open surfaces; this would leave the hatchling directly exposed to mortality factors, resulting in a substantially reduced likelihood of survival. However, if late juvenile or adult snails feed on prey other than the preferred prey type this would only result in smaller net energy gains (cf., Palmer, 1983, 1984; Brown and Richardson, 1987; Hughes and Burrows, 1990; Burrows and Hughes, 1991a), since late juveniles and adults are much less vulnerable to predation and desiccation. Indeed, prey preferences in late juvenile and adult *Nucella emarginata* (Palmer, 1984) and *N. lapillus* (Hughes et al., 1992) are only moderate or weak compared to the preferences of newly hatched *N. emarginata*.

If the distribution of young *N. emarginata* among microhabitats is a consequence of prey preferences, the subsequent shift in microhabitat use from structural refuges to open surfaces, over the sizes of 3–8 mm shell length (Gosselin, 1994), should correspond to a shift in prey preferences. Prey preferences do change at some point during ontogeny, as late juvenile and adult *N. emarginata* preferentially consume mid-sized *Balanus glandula* (Palmer, 1984).

In conclusion, considerations of energy gain can not explain the strong preference of hatchlings for small mussels over other prey species, and thus energy maximization would not be the adaptive reason for this preference. Although such a strong prey preference appears to be related to microhabitat use, further studies of the responses of

hatchlings to prey odours and of ontogenetic changes in prey preferences are necessary to understand fully the significance of prey selection, and may provide an understanding of the mechanisms controlling the distribution of predatory snails throughout ontogeny.

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