

## Feeding habits of newly hatched juveniles of an intertidal predatory gastropod, *Nucella emarginata* (Deshayes)

Louis A. Gosselin\*, Fu-Shiang Chia

Department of Zoology, University of Alberta, Edmonton, Alberta, Canada T6G 2E9, and Bamfield Marine Station, Bamfield, B.C., Canada V0R 1B0

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### Abstract

The feeding habits of juvenile *Nucella emarginata* (= *Thais emarginata*), a marine prosobranch gastropod with direct development, were examined to determine when predatory feeding begins, and if ontogenetic shifts in mode of feeding occur. Most hatchlings did not attack live prey during the first 3 days after emerging from their egg capsule. By day 10, however, over 80% of the hatchlings had attacked prey. The late onset of predatory feeding appears to be ontogenetic, rather than a consequence of handling or experimental conditions. Hatchlings did not use alternate food types (mussel feces, algae, biofilm, or barnacle moults), as determined indirectly by growth, survival, and organic content measurements of hatchlings. Once *N. emarginata* started attacking prey, six species of invertebrates which co-occur with the hatchlings in the field were consumed: three bivalves (*Lasaea* spp., *Musculus taylori*, and *Mytilus* spp.), and three barnacles (*Balanus glandula*, *Chthamalus dalli*, and *Pollicipes polymerus*). Hatchlings did not attack limpets (*Lottia pelta* and *Lottia digitalis*), a littorine (*Littorina scutulata*), the bivalve *Hiatella arctica*, or other hatchlings. In addition, hatchlings were able to survive for up to 120 days without food. Although no ontogenetic shift in mode of feeding was observed in young *N. emarginata*, at least two prey species consumed by hatchlings cease to be used during ontogeny. Possible reasons for the late onset of feeding are discussed.

**Key words:** Hatchling; Juvenile; Onset of feeding; Ontogeny; Predation

### 1. Introduction

The feeding habits of adult gastropods have been extensively studied (see reviews by Hughes, 1980, 1986, and by Crothers, 1985), particularly those of thaidine gastropods (Connell, 1970; Hughes & Dunkin, 1984; Palmer, 1984; Brown & Richardson, 1987;

\* Corresponding author.

Gosselin & Bourget, 1989). Thaidine gastropods feed mainly on mussels and barnacles (Palmer, 1984, 1988; Crothers, 1985). Few studies, however, have examined the feeding habits of very young thaidids. Largen (1967) reported that recently hatched *Nucella lapillus* feed on three species of barnacles and at least six species of molluscs, including conspecifics. Young *N. emarginata* are known to attack the barnacles *Balanus glandula* Darwin and *Chthamalus dalli* Pilsbry (Palmer, 1990). Juvenile snails in both these studies, however, were at least a few weeks old at the time feeding was confirmed and prey were identified. The feeding habits of thaidids during the first days after emerging from their egg capsule have not been examined and no attempts to detect ontogenetic shifts in the mode of feeding have been reported. However, ontogenetic shifts in food use are common among aquatic invertebrates (Neill & Peacock, 1980; Davies et al., 1981; Town, 1981; Werner & Gilliam, 1984; Reid et al., 1990). Few documented cases exist for predatory gastropods, but substantial shifts, where early juveniles and adults depend on different food resources, have been reported. Bernard (1967) found that *Polinices lewisi*, a naticid snail which feeds on clams as an adult, is a herbivore during the first 5 to 6 months of its life. *Retusa obtusa*, an opisthobranch, feeds on radiolaria during the first 5 to 6 months, after which it gradually changes to a diet of the snail, *Hydrobia ulvae* (Berry, 1989). In addition, changes in diet (*N. lapillus*, Hughes et al., 1992) and in drill site (*N. emarginata*, Hart & Palmer, 1987) have been reported for late juvenile thaidids.

In this study, we examine *N. emarginata* (= *Thais emarginata*) (northern) (c.f. Palmer et al., 1990), an intertidal predatory gastropod, to determine: (1) if newly hatched individuals initiate predatory feeding immediately after emerging from their egg capsule, and if not, (2) if newly hatched *N. emarginata* employ non-predatory (alternate) modes of feeding. Also, we determine: (3) which species hatchlings will consume once they have started attacking prey, and (4) if the feeding habits of hatchlings persist through to adulthood. The onset of predatory feeding by this organism can readily be detected as it attacks prey by drilling through their shell, and even brief, incomplete attacks can be recognized (Palmer, 1990; Gosselin, pers. obs.). The term "hatchling" is used here to describe juvenile *N. emarginata* from the moment they emerge from their egg capsule until they reach a shell length of 3 mm.

## 2. Materials and methods

### 2.1. Study site and organism

The present study was carried out in Barkley Sound, British Columbia, Canada. *N. emarginata* adults (15–22 mm shell length) and ripe egg capsules (unplugged capsules containing fully developed individuals that have not yet emerged) were collected at Kirby Point (48°50'85"N, 125°12'40"W), a site exposed to intense wave action; prey were collected at Kirby Point and at Dixon Island (48°51'15"N, 125°06'90"W). Experiments were conducted at the Bamfield Marine Station between June 1990 and July 1992.

*Nucella emarginata* embryos develop within benthic egg capsules. Consumption of nurse eggs is completed before the late veliger stage is reached, and final development is at the expense of their reserves (Leboeuf, 1971). Even when few veligers are present

within a capsule, consumption of nurse eggs ceases well before hatching, and excess nurse eggs remain unused (T. Rawlings, pers. com.). Individuals emerge as crawl-away juveniles. Sizes of newly hatched *N. emarginata* range from 0.9 to 1.8 mm, measured from the apex to the tip of the siphonal canal (Spight, 1976; Gosselin, pers. obs.). For the experiments described herein, we used hatchlings that had been spawned in the field and had undergone complete larval development in their natural environment. Ripe capsules were collected from the field and placed in cages in flowing seawater in the laboratory. Only hatchlings that emerged within 24 h were used in the following experiments, thus ensuring that all hatchlings were of identical age (time of emergence is considered  $t = 0$ ). Hatchlings had no access to potential food items prior to their use in the experiments described herein.

Three cage sizes were used in the course of this study: (1) "large": modified food containers, 95 × 95 × 60 mm; (2) "medium": modified plastic vials, 39 mm diam. × 62 mm long; and (3) "small": modified centrifuge micro test tubes, 11 mm diam. × 14 mm long. All cages were provided with 610  $\mu$ m mesh screening.

## 2.2. Age at first attack

Two experiments were conducted to determine the age at which *N. emarginata* first attacks prey. In these experiments, single hatchlings were placed with three small *Mytilus* spp. (1 to 4 mm shell length) in small cages in flowing seawater. These cages ensured that hatchlings and mussels were in close proximity at all times. After regular time intervals, cages were recovered and each mussel was examined under a dissecting microscope for evidence of predation. A new set of 25 cages was examined for each observation time. Even a slight abrasion of a mussel's shell, by a hatchling that was starting to drill, could be recognized, allowing positive identification of all complete and incomplete attacks. As each cage contained only one hatchling, the proportion of hatchlings attacking prey could be calculated for each period. The first experiment was carried out in March 1992 with newly hatched individuals (<18-h-old); cages were recovered after 5, 10, 15, and 20 days. In the second experiment, carried out in June 1992, cages containing newly hatched individuals were recovered after 1, 3, 5, 7, 10, and 15 days. To verify that the results reflected an actual ontogenetic pattern, unfed 10-day-old hatchlings were placed in the same conditions for 1, 3, and 5 days. Both sets of hatchlings for the June experiment (<18-h and 10-day-old) were obtained from the same sample of egg capsules.

## 2.3. Effects of experimental conditions on the onset of predatory feeding

To determine if the experimental conditions affected the onset of predatory feeding, we modified conditions that appeared most likely to influence foraging behaviour. Specifically, (1) cage size (medium; large); (2) prey type (*B. glandula*; *C. dalli*; *Mytilus* spp.); (3) cage contents (empty; tufts of *Cladophora columbiana* Collins in Setchell and Gardner); and (4) location (laboratory tanks; field). Medium cages each received 10 hatchlings, large cages received 15 hatchlings. *B. glandula*, *C. dalli*, and *Mytilus* were used since they were found to be attacked by juvenile snails in our preliminary trials.

*Cladophora* is an intertidal filamentous algae in which hatchlings are frequently found (Gosselin, pers. obs.). The “field” cages were strapped to boards set in the intertidal zone at Dixon Island. After 5 days all cages were opened and each potential prey item was examined under a dissecting microscope for evidence of attacks by hatchlings. In addition, prey density within each cage was calculated to determine if this factor influenced the outcome of these trials. Prey densities were expressed as numbers of individuals per unit internal surface area of the cage.

#### 2.4. Non-predatory modes of feeding

Use of food types other than live animals (alternate food types) by *N. emarginata* hatchlings was examined indirectly by determining growth, survival, and organic content of hatchlings raised with alternate food types.

##### 2.4.1. Growth and survival

To determine whether hatchlings rely on alternate food types, we compared growth rates and survival of newly hatched individuals raised in five different food type treatments described below. Newly hatched *N. emarginata* were individually marked by applying colour codes to their shell (for method, see Gosselin, 1993). This allowed us to exclude from analysis the data from hatchlings that died during the experiment or were accidentally killed during manipulations. Initially, each hatchling was measured (shell length) and placed in one of the five following treatments:

- (1) *All food*: barnacles (*B. glandula* and *C. dalli*), mussels (*Mytilus* spp.), and *Lasaea* spp.. Unfiltered seawater.
- (2) *No food*: no food item. Filtered seawater.
- (3) *Mussel feces*: feces from *Mytilus edulis* L. and *Mytilus californianus* Conrad were added every 10 days for the first 30 days. Unfiltered seawater.
- (4) *Cladophora*:  $\approx 1 \text{ cm}^3$  of *Cladophora columbiana* was added to the cages. Biofilm was also provided in this treatment by including one rock (unsterilized) collected from the intertidal. Rocks and *Cladophora* tufts were examined initially under a dissecting microscope to ensure no other food items were present. Filtered seawater.
- (5) *Barnacle moults*: moults of *B. glandula* and *C. dalli* were provided every 10 days for the first 30 days. Filtered seawater.

Filtered seawater was obtained by passing water through a  $1 \mu\text{m}$  filter. All food type treatments were replicated in three large cages, with seven hatchlings per cage. Cages were separately placed in aerated 10-l containers without continuous water flow. To prevent hatchlings in the no food, mussel feces, and barnacle moult treatments from having access to diatom or bacterial growth, seawater was UV sterilized. The other treatments also received sterilized seawater to standardize experimental conditions. Seawater was changed approximately every 30 days. Sterilized rocks, boiled for 10 min, were added to all cages to provide a natural substrate. Hatchlings were measured and inspected for mortality after 30 and 50 days. Subsequently, they were periodically examined for mortality until the conclusion of the experiment after 190 days.

#### 2.4.2. Organic content

If hatchlings feed on alternate food sources, their total organic content should be sustained or increased. To examine this, 1-day-old unmarked hatchlings (size range 1.18 to 1.37 mm shell length) were placed in four food type treatments: (1) no food; (2) mussel feces; (3) *Cladophora*; and (4) barnacle moults. These experimental conditions were prepared as in the above growth and survival experiment. On day 1, the organic carbon content of 51 hatchlings (3 per test tube = 17 replicates) was measured by dichromate oxidation against a glucose standard, using the method described by McEdward & Carson (1987). Organic carbon weight ( $\mu\text{g}$ ) of hatchlings, including shells, was then converted to organic matter (OM) by the formula:  $1 \mu\text{g C} = 2.5 \mu\text{g OM}$  (McEdward & Carson, 1987). Organic carbon weight can also be converted to joules to determine the total energy content (McEdward & Carson, 1987). The above method was also used to determine the total organic content of hatchlings after 20 days in each treatment.

#### 2.5. Identification of hatchling prey

To identify the species of live animals which *N. emarginata* hatchlings will consume, 10 species of intertidal invertebrates were separately offered to 15-day-old unfed hatchlings: three cirripedes [*B. glandula*, *C. dalli*, *Pollicipes polymerus* (= *Mitella polymerus*] Sowerby), four bivalves [*Mytilus* spp., *Lasaea* spp., *Hiatella arctica* (L.), *Musculus taylori* (Dall)], two limpets [*Lottia digitalis* (Rathke), *Lottia pelta* (Rathke)], and a snail (*Littorina scutulata* Gould). These species were observed in moderate to high abundances in the field at shore levels where *N. emarginata* is found (Gosselin, pers. obs.). The barnacle *Semibalanus cariosus* (Pallas) was not offered in our trials due to the scarcity of small individuals when hatchlings were available. Each potential prey species was separately offered to single hatchlings in small cages, 15 replicate cages per species. An additional set of 15 cages, each containing four hatchlings, tested for cannibalism. After 5 days in flowing seawater the contents of the cages were examined for evidence of predation.

#### 2.6. Use of hatchling prey by adults

Species successfully attacked by hatchlings were offered to adult *N. emarginata* to determine if adults would consume the same species. These prey species were separately offered to single adults in medium cages, 15 replicate cages per prey species. After 5 days, the contents were inspected for evidence of predation.

### 3. Results

#### 3.1. Age at first attack

Most *N. emarginata* would not attack small *Mytilus* spp. during the first 3 days after emerging from their egg capsule (Fig. 1). The proportion of individuals attacking *Mytilus*

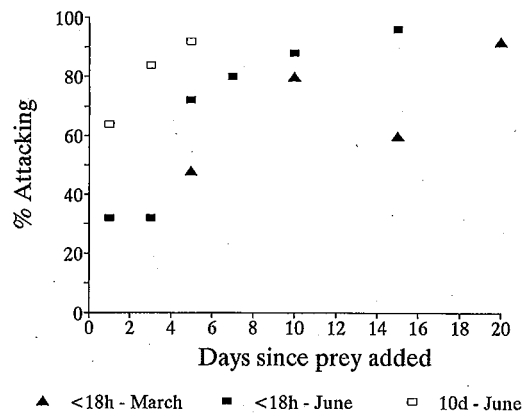


Fig. 1. Percentage of *N. emarginata* hatchlings attacking small *Mytilus* spp.. Hatchlings were individually placed in small cages with three small *Mytilus*. Two sets of hatchlings were placed with prey within 18 h of emerging from their egg capsules, in March and June 1992. A third set of unfed hatchlings were placed in small cages with *Mytilus* 10 days after emergence. Each value was calculated from a separate set of 25 replicates.

Table 1

Number of attacks by *N. emarginata* hatchlings, when placed in 10 different sets of experimental conditions, during the first 5 days after emerging from their egg capsules

Prey species	Conditions			Attacks per hatchling* $\bar{x} \pm SD$
	Cage	Location	Additional contents	
<i>B. glandula</i> (1.2–12.6 mm shell diameter)	Large	Lab.		$0.07 \pm 0.12$
	Large	Field		$0.09 \pm 0.04$
	Medium	Lab.		$0.20 \pm 0.26$
<i>C. dalli</i> (1.1–5.7 mm shell diameter)	Large	Lab.		$0.07 \pm 0.07$
	Large	Field		$0.13 \pm 0.12$
	Medium	Lab.	<i>Cladophora</i>	$0.13 \pm 0.15$
<i>Mytilus</i> spp. (1.0–5 mm shell length)	Large	Field		$0.13 \pm 0.13$
	Large	Lab.		$0.43 \pm 0.32$
	Medium	Lab.	<i>Cladophora</i>	$0.43 \pm 0.40$
	Medium	Lab.		$0.27 \pm 0.12$

Sizes of *B. glandula* and *C. dalli* are shell diameters measured along the rostro-carinal axis. Cage sizes: large =  $95 \times 95 \times 60$  mm (15 hatchlings/cage); medium = 39 mm diam.  $\times$  62 mm long (10 hatchlings/cage). "Field" cages were secured in the intertidal zone for the 5-day period. A small quantity of *Cladophora columbiana*, a filamentous algae, was added to certain cages to provide a typical microhabitat. All experimental conditions were replicated in three cages.

\* Total attacks per cage, including incomplete attacks, was divided by the number of hatchlings per cage to determine the number of attacks per hatchling.

then increased with time: after 10 days, at least 80% had attacked. When unfed 10-day-old hatchlings were placed in the same conditions, however, the proportion of individuals that had attacked prey after 1 day was twice that of newly hatched individuals after one day (Fig. 1). The proportion of 10-day hatchlings that had attacked after 3 days with *Mytilus* (84%) was similar to that of < 18 h hatchlings enclosed for 10 to 15 days with *Mytilus*. There was no significant difference between the sizes of attacking and non-attacking < 18 h hatchlings after one day (ANOVA:  $F = 2.71$ ,  $p = 0.11$ ,  $n = 25$ ) or after 3 days with prey ( $F = 0.49$ ,  $p = 0.49$ ,  $n = 25$ ).

### 3.2. Effects of experimental conditions on the onset of predatory feeding

The highest attack rates (no. of attacks per hatchling) were obtained in cages containing small mussels (Table 1). Even then, however, at least 57% of the hatchlings did not attack prey, although several were found crawling over prey items. In addition, since certain hatchlings will attack 2 or 3 times over a 5-day period (Gosselin, pers. obs.), the proportion of hatchlings that actually attacked prey was probably smaller than the attack per hatchling values. Also, the regression between attack rate and prey density was not significant ( $F = 1.73$ ,  $p = 0.20$ ,  $n = 32$ ; pooled data from all experimental conditions and from the "age at first attack" experiment). Regardless of prey density, prey type, cage size, location of cages, or inclusion of *Cladophora*, most hatchlings did not attack prey during the 5-day period.

Table 2

Initial sizes (age < 24 h) and growth (shell length increment) of *N. emarginata* hatchlings when offered alternate food types

Food type treatment	Initial shell length (mm) <sup>a</sup> $\bar{x} \pm \text{SE}$	Growth Days 0–30 (mm) $\bar{x} \pm \text{SE}$	SNK <sup>b</sup>	Growth Days 30–50 (mm) $\bar{x} \pm \text{SE}$	SNK <sup>b</sup>
All food	1.31 ± 0.04 (18)	0.87 ± 0.10 (18)	A	1.07 ± 0.11 (17)	A
No food	1.42 ± 0.05 (17)	0.03 ± 0.02 (17)	B	0 ± 0 (16)	B
Mussel feces	1.36 ± 0.06 (15)	0.11 ± 0.03 (15)	B	0 ± 0 (14)	B
<i>Cladophora</i>	1.38 ± 0.05 (13)	0.10 ± 0.03 (13)	B	−0.003 ± 0.006 (12)	B
Barnacle moults	1.31 ± 0.04 (18)	0.10 ± 0.02 (18)	B	0.009 ± 0.004 (18)	B
ANOVA $F$	1.12	45.14		82.12	
$p$	0.35	<0.0001		<0.0001	

As a result of mortality, the number of hatchlings per treatment ranged from 12 to 18.

<sup>a</sup> Calculation of average initial hatchling sizes was based on the measurements of individuals still alive on day 30.

<sup>b</sup> Student-Neuman-Keuls grouping at  $\alpha = 0.05$ : means with the same letter are not significantly different.

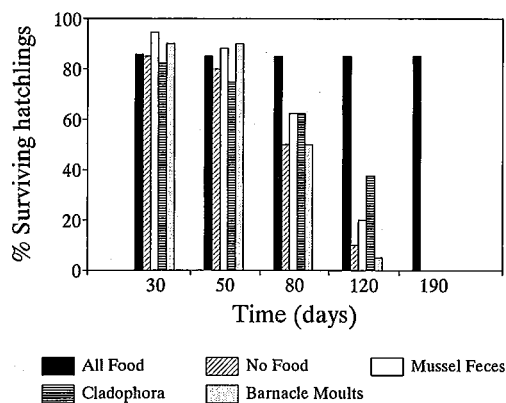


Fig. 2. Survival of *N. emarginata* hatchlings in five food type treatments. Twenty-one hatchlings were initially placed in each treatment. The % surviving hatchlings on day 120 in the mussel feces, *Cladophora*, and barnacle moult treatments were not significantly different from that in the no food treatment ( $G$ -test,  $\alpha = 0.05$ ;  $G$  value adjusted using Williams' correction; Sokal & Rohlf, 1981).

### 3.3. Non-predatory modes of feeding

#### 3.3.1. Growth and survival

Growth of hatchlings in the alternate food type treatments (mussel feces, *Cladophora*, barnacle moults) were not significantly different from hatchlings in the no food treatment during the two consecutive periods (Table 2). Hatchlings in the no food and alternate food type treatments increased in length by an average of 6.15% of initial length during the first 30 days, while hatchlings in the all food treatment grew by an average of 66.4%. Predatory feeding is therefore necessary for substantial growth to occur. In addition, hatchlings in the alternate food type treatments did not survive longer than those in the no food treatment (Fig. 2).

#### 3.3.2. Organic content

The organic content of hatchlings after 20 days in the three alternate food type treatments were not significantly different from that of hatchlings in the no food treatment (Table 3). Yet, the organic content of hatchlings in the no food treatment on day 21 was significantly lower than on day 1 (Table 3), indicating that the 20-day period was sufficient for the organic content to decrease by a measurable quantity.

### 3.4. Identification of hatchling prey

Six species of intertidal invertebrates were attacked by *N. emarginata* hatchlings (Table 4); at least three successful attacks were recorded on each of these species. All hatchlings in the *Mytilus* replicates were successful in drilling through the mussel's shell.



Table 3

Total organic matter (OM) per *N. emarginata* after hatching (day 1) and after 20 days in four food type treatments

	Total OM ( $\mu\text{g}$ )			ANOVA	
	$\bar{x}$	SE	n	F*	p
Day 1	66.61	2.49	17		
Day 21:				6.52	0.017
No food	55.42	3.86	11		
Mussel feces	58.84	5.38	9	1.21	0.368
<i>Cladophora</i>	55.98	3.90	11		
Barnacle moults	63.41	6.00	9		

\* ANOVAs were used to compare OM on day 1 with OM in no food treatment on day 21, and also to compare OM values among the four treatments on day 21.

Only one attack on *Hiatella arctica* was recorded: the borehole was superficial and the shell was not successfully drilled through. Conspecifics were not attacked.

### 3.5. Use of hatchling prey by adults

Adult *N. emarginata* did not attack three of the six species that were consumed by hatchlings (Table 5). While *P. polymerus* was not attacked by adults in the feeding trials, adults have been observed feeding on them in the field, although infrequently (Gosselin, pers. obs.).

Table 4

Number of *N. emarginata* hatchlings (15-day-old) attacking 11 species of intertidal invertebrates

Species	Size range (mm)		No. of attacking hatchlings
	min.	max.	
<i>P. polymerus</i>	1.1	2.7	8
<i>C. dalli</i>	1.9	4.9	12
<i>B. glandula</i>	2.8	5.6	12
<i>Mytilus</i> spp.	1.7	4.3	15
<i>M. taylori</i>	1.0	3.5	8
<i>Lasaea</i> spp.	1.3	3.0	7
<i>Hiatella arctica</i>	3.0	6.8	1
<i>Lottia pelta</i>	1.8	3.6	0
<i>Lottia digitalis</i>	2.1	3.9	0
<i>Littorina scutulata</i>	1.3	5.0	0
<i>N. emarginata</i>	1.0	1.7	0

For each species, 15 small cages each contained one hatchling and three individuals of the listed species for 5 days. The *N. emarginata* treatment consisted of four hatchlings per cage. Sizes of *P. polymerus*, *C. dalli*, and *B. glandula* are shell diameters, measured along the rostro-carinal axis. All other prey sizes are shell lengths.

Table 5  
Number of *N. emarginata* adults (15–22 mm shell length) attacking the prey of hatchling snails

Species	Size range (mm)		No. of attacking snails
	min.	max.	
<i>P. polymerus</i>	8	21	0
<i>C. dalli</i>	2	5	10
<i>B. glandula</i>	2.5	11	15
<i>Mytilus edulis</i>	10	22	15
<i>M. taylori</i>	1.5	4.5	0
<i>Lasaea</i> spp.	2	3.5	0

For each species, 15 medium cages each contained one adult and at least three individuals of the listed species for 5 days. Sizes of *P. polymerus*, *C. dalli*, and *B. glandula* are shell diameters, measured along the rostro-carinal axis. All other prey sizes are shell lengths.

#### 4. Discussion

##### 4.1. Onset of predatory feeding

Even when placed directly on prey items, most *N. emarginata* hatchlings younger than 3 days would not attack. Instead, most began attacking prey 3 to 10 days after hatching. The high proportion of 10-day-old hatchlings that attacked during the first 3 days of enclosure with prey suggest that the proportion of feeding individuals increases with age regardless of handling disturbance. The late onset of predatory feeding persisted despite numerous changes to the experimental conditions.

Premature emergence due to handling disturbance is not believed to be responsible for the low attack rates of newly hatched *N. emarginata*. The collection and handling of the capsules were not likely to produce disturbance in excess of what is normally experienced at Kirby Point, a site frequently subjected to severe wave impaction. Temperature shock was also unlikely, since surface water temperature differed from laboratory water temperature only by  $\approx 1^\circ\text{C}$ . A late onset of predatory feeding by newly hatched *N. emarginata* has been observed consistently in several preliminary feeding trials carried out between 1990 and 1992, with hatchlings from exposed and protected sites in Barkley Sound. Thus, it appears that the late onset of predatory feeding in *N. emarginata* is an actual ontogenetic pattern. Also, this feeding pattern is not likely to reduce hatchling survivorship, as most individuals can survive more than 50 days without prey (Fig. 2).

The late onset of predatory feeding did not correspond to a period of transient use of mussel feces, *Cladophora*, biofilm (included in the *Cladophora* treatment), or barnacle moults. These alternate food types did not increase growth, survival time, or organic content relative to hatchlings that had been starved. Consequently, no ontogenetic shift in mode of feeding was detected in *N. emarginata*.

##### 4.2. Hatchling prey

Of the species that were offered, hatchlings only consumed bivalves (three species) and cirripedes (three species) (Table 4). Drilled empty shells of small individuals of each

of these six species have been found in the field when sampling microhabitats containing hatchlings (Gosselin, pers. obs.). Drill holes were of similar size and position as those produced by hatchlings in the laboratory, suggesting that hatchlings also feed on these organisms in the field.

Adult *N. emarginata* did not consume *M. taylori* and *Lasaea*. This may be due to the small size of these organisms, which have adult shell sizes no larger than 5 mm (Kozloff, 1987). Similarly, adults would not attack *Mytilus* spp. smaller than 5 mm. Yet, adults did consume many *C. dalli* measuring only 3 to 5 mm shell diameter. Therefore, *N. emarginata* may be unable to handle relatively small prey that are not firmly attached to a substratum. Although no ontogenetic shift in mode of feeding was observed in *N. emarginata*, at least two species consumed by hatchlings cease to be used during ontogeny.

#### 4.3. Survival during prolonged periods of starvation

The ability of *N. emarginata* hatchlings to survive for extended periods without food is surprising. Hatchlings can feed on several species that are common intertidally, and are therefore likely to have good access to prey. Prey will be inaccessible, however, if embryos are unable to exit ripe egg capsules. This can occur if the young snail does not fit through the opening, if a capsule mate too large for the opening has blocked the exit, or if the opening is irregular (Gosselin, pers. obs.). In the field, capsular material will break down a few days to several weeks after the capsule has become unplugged (pers. obs.). Given their ability to survive for extended periods without feeding, *N. emarginata* trapped within their egg capsule might survive until the walls deteriorate.

#### 4.4. Conclusions

Predatory gastropods might be expected to start feeding immediately after hatching because rapidly attaining a larger size will reduce their vulnerability to predation, desiccation, and wave action (Faller-Fritsch, 1977; Underwood, 1979) to which very small individuals are highly vulnerable (Branch, 1975; Underwood, 1979; Werner & Gilliam, 1984). An immediate onset of feeding, however, might conflict with other requirements. Juveniles emerging from egg capsules are directly exposed to mortality factors until they reach protective microhabitats. If newly hatched snails stop to attack prey (e.g. by drilling through a prey's shell) before reaching a refuge, they extend the period of direct exposure to these mortality factors. We found that the shortest time required for 20-day-old *N. emarginata* hatchlings to drill, consume, and discard a small mussel (1–2 mm shell length) was 22 h (unpubl. data). Some had not yet discarded their prey after 48 h. Thus, if newly hatched *N. emarginata* stop to attack prey before reaching a refuge, they remain exposed to mortality factors during at least two tidal cycles. The main requisite early in life may be to find protection while living off reserves remaining from the egg capsule (Feare, 1970). However, the onset of feeding does not appear to be triggered by external cues, such as finding a refuge; attack rates were not higher when hatchlings were placed in cages with *Cladophora*, in field cages, or in various other conditions (Table 1). Alternatively, the late onset of feeding may serve to prevent or

reduce cannibalism within the egg capsule (cannibalism by *N. lapillus* embryos was reported by Largen, 1967, and we have observed one case of predation within the egg capsule in *N. emarginata*). The late onset of predatory feeding could also be an indirect consequence of selective pressures to minimize encapsulation time, whereas hatchlings would emerge once fully mobile but before a complete development of the feeding apparatus (e.g. the radula). Additional information on the development, behaviour, and ecology of young juveniles is necessary to fully understand the causes and mechanisms producing the late onset of feeding in *N. emarginata*.

## 5. Acknowledgements

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