

An ecological transition during juvenile life in a marine snail

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ABSTRACT: Ecological shifts occurring after metamorphosis in benthic marine invertebrates have received much less attention than the more conspicuous transition occurring at metamorphosis and settlement. It remains unclear whether postmetamorphic shifts occur simultaneously or at different times, and whether the shifts occur over brief, discrete periods or are extended or even continuous through juvenile life. The present study of the muricid gastropod *Nucella emarginata* examines the ontogeny of vulnerability to desiccation, of susceptibility to hatchling predators, of shell coloration, and of distribution among microhabitats as a function of snail size. All the above parameters changed substantially over approximately the same size range. Individuals acquired the ability to survive direct exposure to desiccation for the duration of a low tide over the 3.1–6.5 mm shell length (SL) size range, and also became virtually invulnerable to hatchling predators when they reached 6.5 mm SL. The shift in mortality factors was paralleled by a change in shell colour over the 3–7 mm SL size range, and in distribution over the 3–8 mm SL size range. All shifts were therefore completed by the time individuals reached 8 mm, or by the age of ~4 mo based on growth rates in the laboratory. The coordination of these ecological changes in *N. emarginata* over the 3–8 mm SL size range constitutes an ecological transition that partitions postmetamorphic life into 2 periods, early juvenile and late juvenile/adult, each with distinct selective environments and corresponding adaptive traits. A similar ontogenetic transition has also been documented in juvenile lobsters, and studies of juveniles of other species reveal that comparable ecological changes are common among benthic marine invertebrates. Interspecific variation is nevertheless expected in the exact nature and timing of the transition, particularly as a result of differences in initial juvenile size, growth rate, adult size, ability to learn, and motility.

KEY WORDS: Early juvenile · Ontogeny · Selective pressures · Life history · Mortality factors

INTRODUCTION

The most conspicuous ontogenetic shift in many marine invertebrates occurs at metamorphosis. Major ecological changes, including a shift from pelagic, encapsulated or brooded existence to that of an independent benthic individual, occur at about the same time as anatomical changes transform the larva or embryo into a young juvenile. This ecological transi-

tion is important because it constitutes a radical change in the nature and intensity of selective pressures within the life of each individual.

Although the changes occurring at metamorphosis are often striking, significant but less conspicuous ecological shifts can also occur during postmetamorphic life. As emphasized by Werner & Gilliam (1984), shifts in diet and distribution are common among juvenile aquatic animals. Ontogenetic shifts occurring after metamorphosis in marine invertebrates have nevertheless received much less attention than events occurring at metamorphosis and settlement. It therefore remains unclear whether postmetamorphic shifts occur simultaneously or at different times, and whether the

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shifts occur over brief, discrete periods or are extended or even continuous through juvenile life. It is important to establish the timing of these shifts to understand the significance of juvenile traits and of ontogenetic changes in traits.

The present study examines the timing of major ontogenetic shifts in the muricid gastropod *Nucella emarginata* (Deshayes) (northern species, as defined by Palmer et al. 1990). Recent studies of this species have revealed differences between early juveniles and adults in diet (Gosselin & Chia 1994, 1996), mortality factors (Gosselin & Chia 1995a), and in distribution (Gosselin & Chia 1995b). The latter 2 features are examined in detail in this study.

To survive, newly hatched *Nucella emarginata* must avoid 2 types of mortality factors which seldom constitute a threat to adults (Gosselin & Chia 1995a). First, newly hatched *N. emarginata* are unable to survive direct exposure to desiccation for the duration of a low tide, contrary to adults. Secondly, hermit crabs and small shore crabs are the main predators of hatchlings but these predators are not a threat to adult snails, while predators of adult snails do not feed on hatchlings. The distribution of hatchlings and adults among intertidal microhabitats also differs (Gosselin & Chia 1995b). Virtually all hatchlings are cryptically located within structurally complex microhabitats (tufts of filamentous algae, mussels clusters, densely packed barnacles), whereas adults are mostly located on open surfaces.

The above information indicates that several shifts take place during postmetamorphic life in *Nucella emarginata*. The present study examines the ontogenetic timing of these transitions. Specifically, this study documents the ontogeny of vulnerability to desiccation and of susceptibility to hatchling predators, 2 of the main selective pressures at the onset of postmetamorphic life (Gosselin & Chia 1995a). Also examined is the ontogeny of shell coloration, a parameter that has been associated with predation and physiological stress (Mercurio et al. 1985, Etter 1988, Smith & Herrnkind 1992). Finally, data on distribution throughout the postmetamorphic period, recently reported by Gosselin & Chia (1995b), will be examined in the 'Discussion'.

MATERIALS AND METHODS

Study site and organism. The observations and experiments presented herein were carried out at the Bamfield Marine Station and at nearby field sites in Barkley Sound on the

west coast of Vancouver Island, British Columbia, Canada (Fig. 1). Newly hatched *Nucella emarginata* were obtained by collecting ripe egg capsules (unplugged capsules containing metamorphosed individuals that had not yet emerged) from the field and placing them in cages in flowing seawater in the laboratory. Only the hatchlings that emerged during the first 24 h in the laboratory were used. Snails ≥ 2 mm shell length (SL) were collected from Ross Islets (Fig. 1).

Ontogeny of vulnerability to desiccation. To determine when *Nucella emarginata* acquires the ability to withstand desiccation stress for the full duration of a low tide period, snails of a range of sizes were exposed to a controlled environment simulating field conditions at low tide. The experiment was carried out in August 1992 within 24 h of collecting the snails. Size classes consisted of newly hatched snails (1.0–1.5 mm SL), larger juveniles (2.1–3.0, 3.1–5.0, and 6.5–9.0 mm SL), and adults (18.0–26.0 mm SL). The snails were placed on shale rock plates (40 × 40 × 3 cm), wetted with seawater, in an incubator at 22°C. This air temperature is typical of the intertidal zone at low tide in Barkley Sound on a warm day (Gosselin & Chia 1995a). A fan in the incubator maintained a moderate air flow throughout the experiment. Relative humidity within the incubator decreased from 86% at the start of the experiment to 77% after 8 h, values that are comparable to levels observed in the intertidal zone at low tide (Gosselin & Chia 1995b). A separate set of each size class of snails were recovered after 1, 2, 4, 6, and 8 h. Sample sizes for each observation interval were as follows: 1.0–1.5 mm = 15 snails; each other size class = 10 snails. Due to limited availability, however, only 1 set of 2.1–3.0 mm and 6.5–9.0 mm snails were used; these were recovered only at the end of the 8 h experiment. Once removed from the incubator, snails were immediately placed in flowing seawater for 30 min, after which each individual was examined. Individuals not responding when the operculum was touched with a probe were recorded as dead.

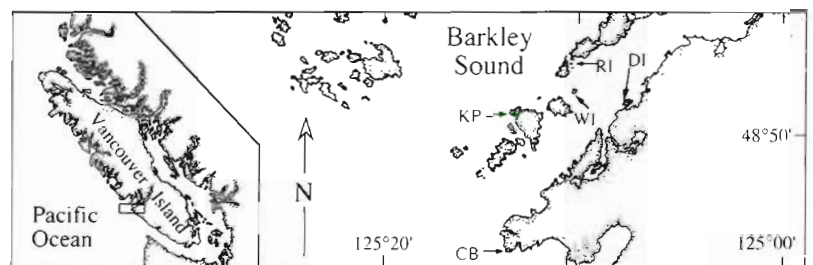


Fig. 1. Map of Barkley Sound (off British Columbia, Canada) showing study sites. CB: Cape Beale, DI: Dixon Island, KP: Kirby Point, RI: Ross Islets, WI: Wizard Islet

Ontogeny of susceptibility to hatchling predators.

Three steps were necessary to document the ontogeny of susceptibility to hatchling predators: (1) establish the relationship between predator size and the size range of snails they will consume, (2) determine the size-frequency distribution of predators in the field, and (3) calculate a predation susceptibility index for each snail size based on (1) and (2). The term 'susceptibility' is used here to represent a combined measure of vulnerability (see Gosselin & Chia 1995a) to predators and of abundance of the predators in the field. Susceptibility will be high if individuals are vulnerable to given predators and these predators are abundant. Details of each of the 3 steps are as follows.

Predator size-snail size relationship: This first step defined the relationships between predator size and the maximum and minimum snail sizes they will consume. In turn, this allowed the determination, for a snail of any given size, of the range of predator sizes capable of killing it. Three hatchling predators (*Hemigrapsus nudus*, *Pagurus hirsutiusculus*, and *P. granosimanus*) of a broad range of sizes were collected in the intertidal zone. These decapod crustaceans, particularly *P. hirsutiusculus* and *H. nudus*, constitute the most abundant and often the only predators likely to be an important threat to hatchling *Nucella emarginata* in Barkley Sound (Gosselin & Chia 1995a). A third hermit crab species, *P. samuelis*, was infrequently found in the field and was not included in these experiments. Predators with intact claws were brought to the laboratory, measured [claw length (CLL) from the base of the propodus to its tip, and claw width (CLW) measured just below the insertion point of the dactylus], and individually placed in cages (95 × 95 × 60 mm, with 610 µm mesh screening) in flowing seawater. *N. emarginata* were also collected and separated into 1 mm size classes.

Individual predators were offered snails from 6 September to 26 October 1992. The experiment included 20 individuals of each predator species, although 3 *Pagurus hirsutiusculus* moulted during the study and their results were not used. Snails and shell fragments remaining in each cage were recovered every 2 d and a new set of 3 snails was added. When a predator had killed at least 1 snail it was then offered snails of the next larger size class. If a predator had not killed any of the snails, it was offered a new set of snails of the same size a second time. The same approach was used to determine the smallest *Nucella emarginata* that a given predator would kill.

Equations describing the relationships between predator size and consumed snail size were then determined by regression analysis. Predators that did not kill snails were not included in the regression analysis but were taken into consideration when calculating the predation susceptibility index.

Size-frequency distribution of hatchling predators

in the field: The size-frequency distribution of hatchling predators in areas populated by *Nucella emarginata* was assessed at Ross Islets, Wizard Islet, and Dixon Island (Fig. 1) (low-moderate, moderate, and moderate-high exposure to wave action, respectively). Predators were sampled between 16 August and 7 September 1993, a time of the year when hatchling *N. emarginata* and a wide range of juvenile sizes are usually present in the field (Gosselin 1994). Five quadrats (25 × 25 cm) were sampled at 1 m intervals along each of 2 transects running parallel to the shore at 1.2 to 1.8 m above mean lower low water (10 quadrats per site). The length of the right claw of each *Hemigrapsus nudus* and *Pagurus* spp. found within these quadrats was measured. If the right claw was missing or was visibly smaller than the left one, the left claw was measured. No measurements were taken on predators lacking both claws.

Predation susceptibility index: To determine how susceptibility to hatchling predators changes as the snails grow, a predation susceptibility index was calculated. The index value for a given snail size represents the density of hatchling predators in the field that would feed on a snail of this size. The 4 steps in assessing the value of the index for a given snail size were as follows: (1) the range of *Hemigrapsus nudus* sizes capable of killing snails of this size was defined from the snail size versus *H. nudus* size equations determined earlier, (2) field densities of *H. nudus* within this size range were determined using size-frequency data from the field sites. This density value was then reduced to account for the proportion of *H. nudus* that would not attack snails in the laboratory experiments (see example in 'Results' section), (3) the first 2 steps were repeated for each *Pagurus* species, and (4) the resulting densities of each predator species were totalled to produce the index value for the given snail size at one field site. The index value was calculated in this way for each of the 3 sites at which size-frequency distributions of predators had been assessed. The predation susceptibility index does not represent the exact intensity of predation on *Nucella emarginata* in the field because it attributes an equal weight to each individual predator and because the predation experiment was conducted in artificial settings. Nevertheless, the index should constitute a good relative basis for comparison among snail sizes.

Ontogeny of shell coloration. Changes in shell colour were documented for *Nucella emarginata* collected at Ross Islets throughout September and October 1992. All snails smaller than 14 mm SL [i.e. the full size range of immature snails (Palmer 1985)] were measured and the shell colour (white, intermediate, black) and pattern (banded or uniform) were recorded

within 24 h of collection. Brown, grey, and orange shells were recorded as intermediate. Because new shell growth is deposited along the lip of the aperture, observations at this site reveal when the snails begin to incorporate a different colour into their shell. The shell's appearance from the perspective of a nearby observer (or predator), however, remains mostly unchanged until the new pigmentation reaches higher up on the main body whorl through continued growth. The colour and pattern were therefore examined on 2 areas of each shell: the outer lip of the aperture and the area of the main body whorl facing away from the substratum (top of whorl).

RESULTS

Ontogeny of vulnerability to desiccation

When exposed to desiccation, all snails ≤ 3 mm SL died within 8 h (Fig. 2). Survival increased with increasing size over the 3.1–6.5 mm SL size range: 30% of 3.1–5.0 mm snails were still alive after 8 h, and all snails ≥ 6.5 mm survived exposure to desiccation for the full duration of the experiment (Fig. 2). The rock plates on which the snails were placed dried out after 4 to 6 h, which corresponds to the time when the smallest snails died (Fig. 2).

Ontogeny of susceptibility to predators

Predator size - snail size relationship. The size of the smallest snail killed did not scale with predator size.

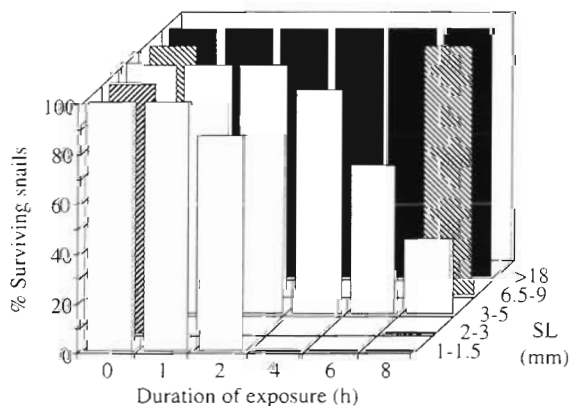


Fig. 2. *Nucella emarginata*. Survival time of snails exposed to desiccation for up to 8 h at 22°C as a function of shell length (SL). Each value represents the survival of a separate set of 1.0–1.5 mm (n = 15) or larger snail sizes (n = 10 per size class). For 2.1–3.0 and 6.5–9.0 mm size classes, survival was determined only for the full 8 h exposure period

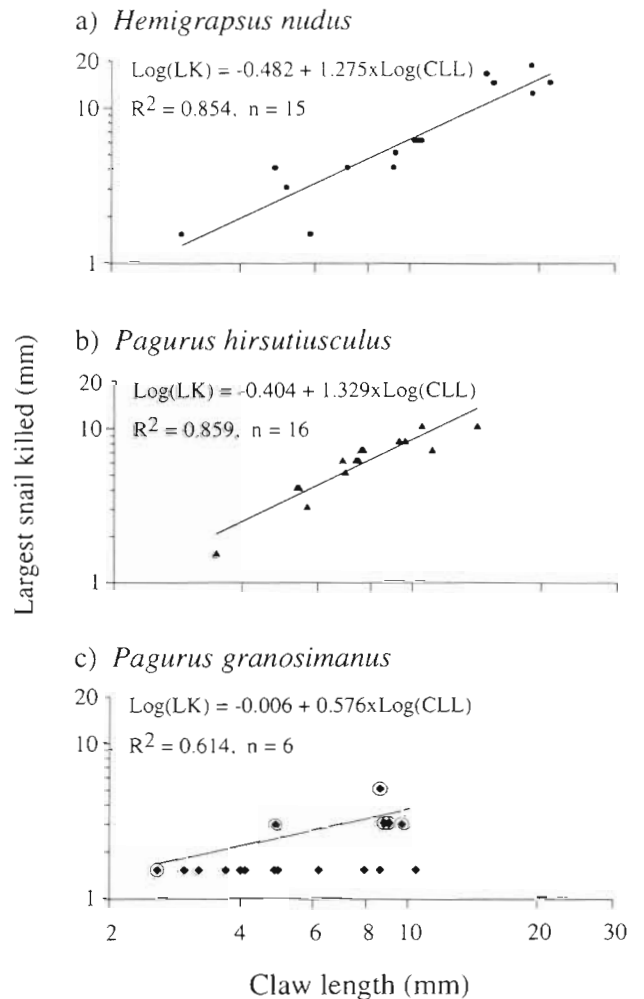


Fig. 3. Relationship between log transformed predator claw length (CLL) and size of largest *Nucella emarginata* killed (LK). Because most *Pagurus granosimanus* only attacked newly hatched snails (~1.5 mm shell length), the regression equation was calculated using only 6 values, indicated by circles (see text). All regression equations were significant (p < 0.001)

The largest *Pagurus hirsutiusculus* and *P. granosimanus*, as well as *Hemigrapsus nudus* measuring up to 19.2 mm CLL, consumed newly hatched *Nucella emarginata*. Only the 2 largest *H. nudus*, 21.1 mm and 25.0 mm CLL, did not attack hatchlings. The size of the largest snail killed, however, did scale with predator size. For this relationship, CLL measurements provided a better fit than CLW. The correlation was also improved by using log transformations of predator and prey sizes. The regression equations between CLL and size of largest snail killed were highly significant (p \leq 0.001) for *H. nudus* and *P. hirsutiusculus* (Fig. 3a, b). Many *P. granosimanus* only attacked hatchlings. Consequently, the regression between CLL and largest

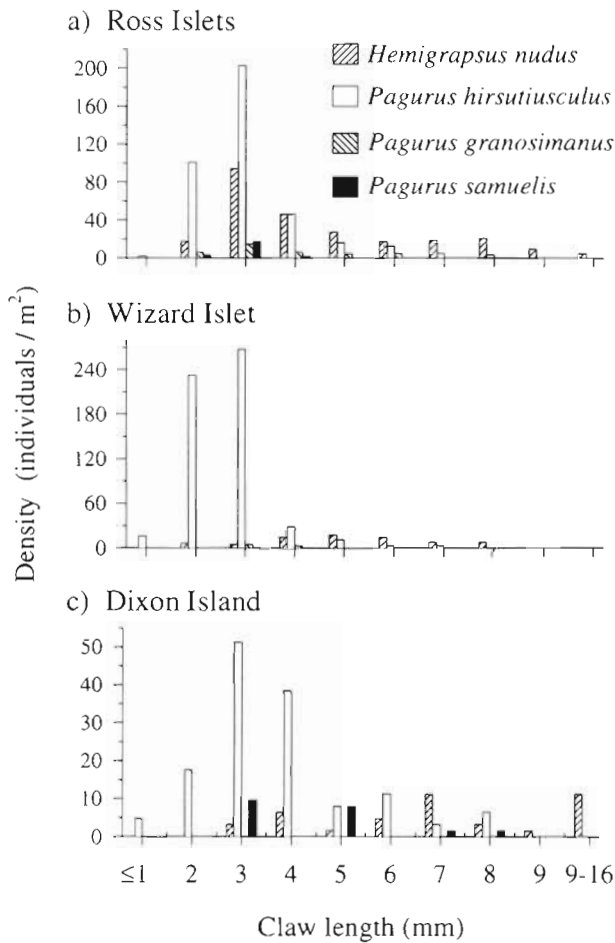


Fig. 4. Size-frequency distribution of hatchling predators at 3 field sites in August and September 1993. Measurements were generally taken on the predator's right claw. Each unit of the horizontal axis (claw length) represents the 1 mm interval preceding the listed value (e.g. 1.1–2.0 mm listed as 2 mm)

snail killed was calculated using results from 5 *P. granosimanus* that did attack larger snails and from the smallest *P. granosimanus* (Fig. 3c). The proportion of *P. granosimanus* not attacking snails >1.5 mm was then taken into account when calculating the predation susceptibility index.

Size-frequency distribution of hatchling predators in the field. Within areas populated by *Nucella emarginata*, *Pagurus hirsutiusculus* was always the most abundant hatchling predator (Fig. 4); relatively few *P. granosimanus* and *P. samuelis* were present. The size range of predators was roughly similar at all sites. All *Pagurus* spp. were smaller than 9 mm CLL, and most were within the 1.1–5.0 mm size range (Fig. 4). *Hemigrapsus nudus* did not exceed 15.9 mm CLL.

Predation susceptibility index. The predation susceptibility index decreased with increasing snail size, reaching zero for snails measuring ≥ 7.5 mm SL at Wiz-

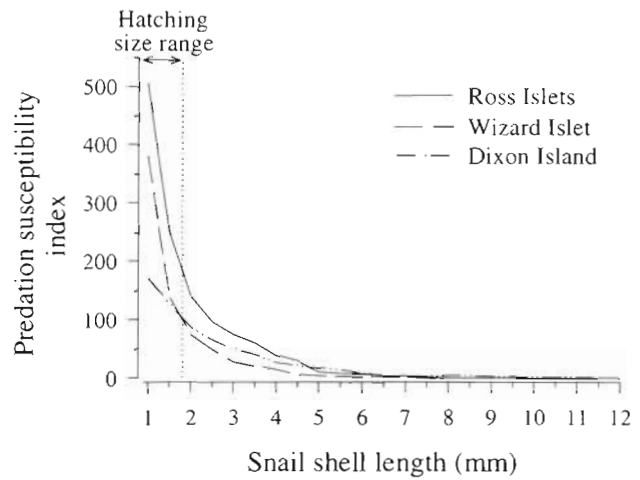


Fig. 5. Susceptibility of *Nucella emarginata* to hatchling predators as a function of shell length. The predation susceptibility index consists of the density (ind. m⁻²) of all hatchling predators that would kill a snail of the given size. Index values were calculated for every 0.5 mm shell length size increment

ard, ≥ 8.0 mm at Ross, and ≥ 11.5 mm at Dixon (Fig. 5). At these sizes, the snails had become invulnerable to hatchling predators. At all sites, however, the index reached values near zero among snails ≥ 6.5 mm SL.

Adjustments were necessary when calculating the index to account for the proportions of predators that would not kill snails in the laboratory experiment. In the *Hemigrapsus nudus* experiment, the smallest crab (2.9 mm CLL) killed 1.0–1.5 mm and 2.1–3.0 mm snails. However, 21.1% of the crabs did not kill any snail even though they were clearly large enough to do so. Field density values for *H. nudus* were therefore reduced by 21.1% when calculating index values. For example, a snail measuring 3 mm SL could be killed by all *H. nudus* ≥ 5.65 mm CLL based on the equation in Fig. 3a. At Ross Islets there were 62.4 *H. nudus* m⁻² that fit in this size range, but since 21.1% of *H. nudus* would not kill snails, only 49.2 m⁻² of those crabs were expected to constitute a threat to a 3 mm snail. This reduced value was used in the determination of the predation susceptibility index. Among *Pagurus granosimanus* ≥ 4.9 mm CLL, 50% of these hermit crabs only killed hatchlings (1.5 mm SL) (Fig. 3). Consequently, field densities of *P. granosimanus* ≥ 4.9 mm CLL were reduced by 50% when calculating the index value for snails >1.5 mm SL. No correction was needed for *P. hirsutiusculus*.

Observations of shell fragments from snails killed by 5 *Pagurus samuelis* under the same laboratory conditions as the other predators indicate that this hermit crab crushes snail shells in the same way as *P. hirsutiusculus*. The equation relating CLL to the largest snail killed for *P. hirsutiusculus* was therefore also used

for *P. samuelis* when determining the predation susceptibility index. Although this may not be fully accurate, it would only have a small effect on the index value because of the low density of *P. samuelis* at all 3 sites.

Ontogeny of shell coloration

The proportion of *Nucella emarginata* with entirely white shells decreased from 100% at hatching to essentially 0% at 6.1–7.0 mm SL (Fig. 6); only 1 out of 188 snails >6 mm was white. Non-white pigmentation was first observed in new shell growth among 2.1–3.0 mm snails (Fig. 6a). In most cases, these pigments were initially incorporated as very lightly coloured radial bands. The width of the bands and the density of the colour then gradually increased with snail size; often, the pigmented bands eventually merged and

subsequent shell growth was uniformly coloured. The density of pigmentation also increased, in many cases becoming black.

Changes in the appearance of the snails, as apparent from the top of the body whorl, occurred mainly over the 3–7 mm SL range (Fig. 6b). The whorls of most 2.1–3.0 mm snails (79%) were still completely white. The proportions of each colour and pattern then changed rapidly up to the 7 mm size, and roughly levelled off among larger size classes (Fig. 6b).

DISCUSSION

Ecological transition in *Nucella emarginata*

The shifts documented herein all occurred over approximately the same size range. The transition in mortality factors was largely completed once *Nucella emarginata* reached 6.5 mm SL. Individuals acquired the ability to survive direct exposure to desiccation for the duration of a low tide over the 3.1–6.5 mm SL size range, whereas susceptibility to hatchling predators decreased gradually with increasing snail size, with individuals becoming virtually invulnerable to hatchling predators once they reached 6.5 mm SL. The transition in mortality factors was paralleled by a shift in shell coloration, which occurred mainly over the 3–7 mm SL size range.

As growing *Nucella emarginata* were gradually released from the restrictions imposed by desiccation stress and hatchling predators, their occurrence outside of structurally complex microhabitats increased, as shown by data reported by Gosselin & Chia (1995b). At the 3 study sites (Ross Islets in 1992 and 1993, Wizard Islet in 1991 and 1992, and Cape Beale in 1992), snails ≤ 8 mm SL were mostly located within complex microhabitats. Individuals >8 mm SL, however, were almost exclusively located on open surfaces. Pooled data from all sites and years (Fig. 7) reveals that the proportion of individuals on open surfaces increased noticeably among snails >3 mm SL, but a majority of individuals in the 3–8 mm SL size range remained within complex microhabitats. The transition to open surfaces was completed when the snails reached 8 mm SL. This conclusion is consistent with field observations during 4 yr of field work at various sites in Barkley Sound (1990 to 1993, author's pers. obs.). Also, many large snails remained conspicuous on open surfaces even at sites where microhabitats capable of concealing them were abundant (e.g. extensive beds of large *Mytilus californianus* at Cape Beale). The change in distribution of *N. emarginata* thus represents an ontogenetic shift largely independent of microhabitat availability.

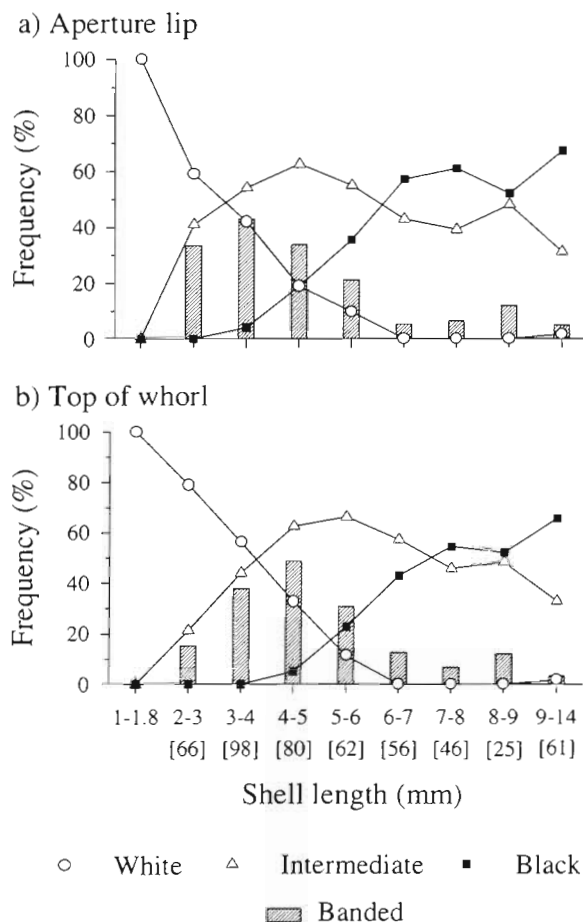


Fig. 6. *Nucella emarginata*. Frequency of colour type and banded pattern on 2 areas of the shell of snails as a function of shell length. Values in brackets are sample sizes for each size class. The 'intermediate' category includes grey, brown, and orange colours

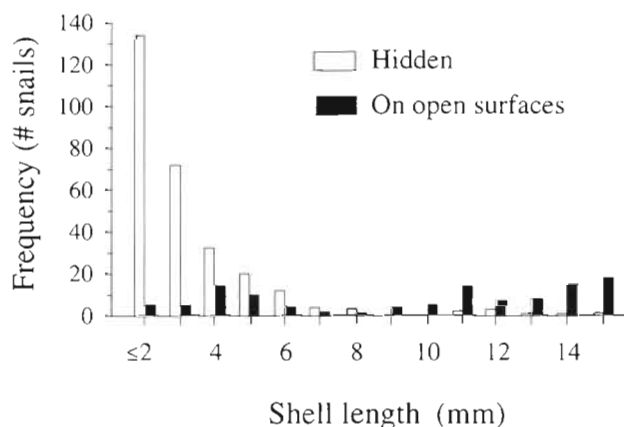


Fig. 7. *Nucella emarginata*. Distribution of snails ($n = 353$) on open surfaces or in structurally complex microhabitats. Pooled data from Ross Islets (1992 and 1993), Wizard Islet (1991 and 1992) and Cape Beale (1992). Data from Gosselin & Chia (1995b)

An important ecological transition therefore begins when *Nucella emarginata* reach ~ 3 mm SL and is completed, at the latest, when individuals reach 8 mm (Fig. 8). In the laboratory, 3 and 8 mm SL sizes were reached after ~ 2 and 4 mo, respectively (Gosselin 1993); growth in the field, however, is probably slower.

Causes of ontogenetic changes during postmetamorphic life in *Nucella emarginata*

Body size is an important determinant of the nature and outcome of an organism's interactions with its environment (Vermeij 1972, Schmidt-Nielsen 1984, Werner & Gilliam 1984). Growth, which is itself an ontogenetic change, may often be the most important driving force of ecological changes. For example, young *Nucella emarginata* emerge from their egg capsule at an average shell length of ~ 1.2 mm (Spight 1976, author's pers. obs.). By the time the snails reach 8 mm SL (i.e. at completion of the ecological transition) their body mass has increased ~ 250 times (Fig. 9). A fully grown adult (25 mm SL) has a body mass roughly 6700 times greater than at the time of hatching. These substantial increases in body size reduce the animal's rate of water loss by decreasing the surface/volume ratio. The size increase, combined with a thicker shell, also make the individual more difficult to handle or crush by small predators. The size change may also alter the snail's energy requirements as well as its ability to grasp and drill prey, and restrict access to the smallest refuges.

Body size, however, is not the only parameter capable of generating ontogenetic changes in *Nucella emarginata*'s ecology. Acquired knowledge of the

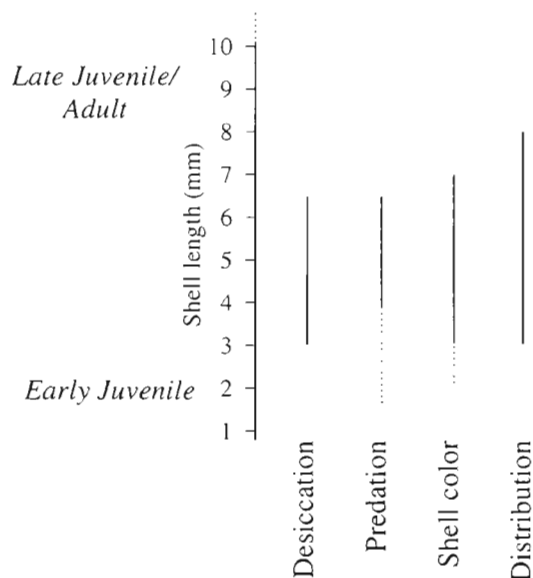


Fig. 8. Summary of results for the 4 factors that were examined, showing the size interval (vertical lines) over which the ontogenetic shifts in *Nucella emarginata* occurred

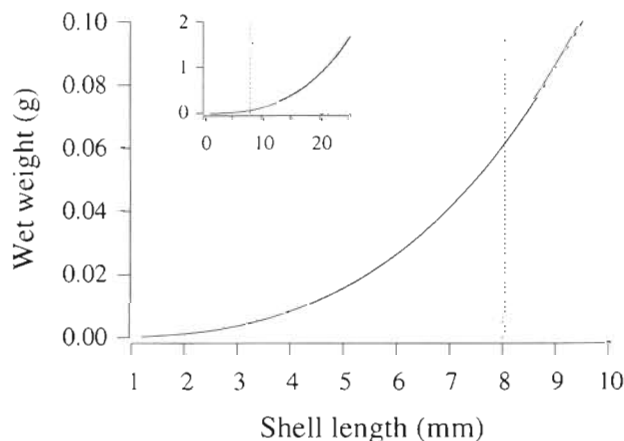


Fig. 9. *Nucella emarginata*. Relationship between snail total body mass (wet weight, WW) and shell length (SL), based on data from Palmer (1982). The equation is: $WW = 0.000146 \times 10^{2.902 \log(SL)}$, $r^2 = 0.992$, $n = 19$

immediate environment influences decision-making in thaidid gastropods (e.g. when selecting prey: Morgan 1972, Dunkin & Hughes 1984, Palmer 1984) and may thus be partly responsible for ontogenetic changes in behaviour. Recently hatched individuals have little information on their surroundings and are most likely to rely on pre-established response patterns or depend on very incomplete information (Gosselin & Chia 1996). During the following months, however, *N. emarginata* acquire information on the habitat in which they

live, and this information can be used to alter the way they interact with their environment (Palmer 1984).

Body coloration of aquatic organisms is often associated with differential mortality due to visual predators (Mercurio et al. 1985, Smith & Herrnkind 1992). White hatchlings were indeed difficult to distinguish from the white shell fragments and sand grains that accumulate in filamentous algae and mussel clusters, and from the grainy white surface of the shells of large barnacles *Semibalanus cariosus*. Alternatively, shell coloration may act to reduce physiological stress (e.g. Etter 1988).

The close correspondence between the shift in distribution and the shift in vulnerability to early juvenile mortality factors suggests microhabitat use could be directly linked to the intensity of these mortality factors. This is consistent with previous reports suggesting a link between habitat shifts and changes in susceptibility to predators in snails (Martel & Chia 1991), scallops (Pohle et al. 1991) and crabs (McMillan et al. 1995). This supports the hypothesis that shelter requirements can be the main determinant of microhabitat use during early juvenile life (Gosselin & Chia 1995b).

Hatching size

The predation susceptibility index suggests an additional conclusion regarding size at hatching. Susceptibility to hatchling predators decreased rapidly over the range of sizes at which *Nucella emarginata* hatch (~0.9–1.8 mm) (Fig. 5). This was due to a pronounced skewness of predator size distributions at the time of sampling towards small individuals capable of killing only the smallest hatchlings. These results indicate that predation by decapod predators can constitute a strong selective pressure favouring a larger size at hatching, as previously suggested (Spight 1976, Rivest 1983), even though all newly hatched snails are vulnerable to these predator species. In addition, the rate of decrease in susceptibility as a function of snail size differed from site to site, suggesting that different populations may experience different levels of intensity of this pressure. If among-site differences in predator population structure persist through time, if the selective pressure imposed by decapod predators is important relative to other pressures on size at hatching, and if the trait is heritable, then differences among sites in size at hatching should be predictable based on determinations of the predation susceptibility index. Further study of the correspondence between the predation susceptibility index and average size at hatching are needed to verify this hypothesis.

Early juvenile ecology

Young juveniles have previously been referred to as 'miniature adults' (Gibbs 1984), and the term 'adult' has frequently been used to refer to all of postmetamorphic life (Vance 1973, Crisp 1974, Rieger 1994, Alexander & Roughgarden 1996), implying that life throughout this period is regulated by a consistent set of processes. The information obtained for *Nucella emarginata*, however, suggests that is not the case. *N. emarginata*'s selective environment as well as some of the animal's traits shift considerably during juvenile life long before reaching maturity. Similarly, pronounced ontogenetic shifts in distribution, vulnerability to predators, behaviour, and body coloration have been reported in juvenile lobsters [*Homarus americanus* (Lavalli & Barshaw 1986, Lawton 1987, Wahle & Steneck 1991, 1992, Cobb & Wahle 1994), *Panulirus argus* (Herrnkind & Butler 1986, Smith & Herrnkind 1992)], and those findings led to the conclusion that early juvenile lobsters were ecologically distinct from adults (see Hudon 1987, Barshaw & Bryant-Rich 1988, Wahle & Steneck 1991, Smith & Herrnkind 1992).

It is becoming increasingly apparent that many species profoundly change the way they interact with their environment during postmetamorphic life. Growth of benthic invertebrates during the postmetamorphic period often leads to size increases of 2 to 4 orders of magnitude [e.g. lobsters (Wolff 1978), mussels (Suchanek 1981), snails (this study)]. Such spans in body size can produce substantial ontogenetic differences in vulnerability to mortality factors. Vulnerability to desiccation and heat stress, for instance, are inversely related to body size in the snail *Nerita scabricosta* (Garrity & Levings 1984) and in 3 species of barnacles (Foster 1971). In addition, many predators feed specifically on small size classes of prey populations, which can lead to pronounced changes in predation pressure on the survivors as they grow (Osman et al. 1990, 1992, Ojeda & Dearborn 1991, Osman & Whitlatch 1995).

Shifts in distribution have been reported for several species. Ontogenetic shifts from structurally complex microhabitats to more open areas occur in mussels [*Mytilus edulis* (Bayne 1964)], snails [*Lacuna vincta* (Martel & Chia 1991)], nudibranchs [*Aplysia juliana* (Sarver 1979)], isopods [*Dynamene bidentata* (Arantes & Anadón 1990)], crabs [*Cancer magister* (Fernandez et al. 1993, McMillan et al. 1995)], seastars [*Acanthaster planci* (Zann et al. 1987)] and urchins [*Strongylocentrotus franciscanus* (Tegner & Dayton 1977)]. Shifts in distribution can also involve changes in height of attachment above the substratum, as in the scallop *Argopecten irradians* (Pohle et al. 1991).

Diets can also shift substantially. Urchins [*Strongylocentrotus purpuratus* (Rowley 1990)] and abalone

[*Haliotis* spp. (Hooker & Morse 1985)] feed on surface films (mainly diatoms) during the first few months after settlement, then change to kelp or other macroalgae. In predatory species diet shifts can be more radical, changing from herbivorous to carnivorous feeding, as in the snail *Polinices lewisi* (Bernard 1967) and the seastar *Acanthaster planci* (Zann et al. 1987, Keesing & Halford 1992). Ontogenetic diet shifts are likely to be common, if only in the size of consumed particles.

Ontogenetic shifts during postmetamorphic life are therefore sufficiently pronounced and widespread that the early juvenile period can be considered an ecologically distinct phase of life in many macrobenthic species.

CONCLUSION

In *Nucella emarginata*, ontogenetic shifts in vulnerability to desiccation, in susceptibility to hatchling predators, in shell colour, and in distribution occurred simultaneously over the 3–8 mm shell length size range. The co-occurrence of these changes over this discrete period constitutes an ecological transition that partitions postmetamorphic life into 2 periods, early juvenile and late juvenile/adult, each with distinct selective regimes and corresponding adaptive traits. Since mortality early in juvenile life is often extremely high (see Gosselin & Qian 1997), the intense selective pressures experienced during that period can be important in shaping population parameters as well as the evolutionary history of the species.

Although ecological shifts appear to be common among benthic invertebrates, variation among species is expected in the exact nature of the transition as well as in the time and rate at which it occurs. This variation will be associated with interspecies differences in initial juvenile size, growth rate, adult size, ability to learn, and motility. Since the potential for behaviorally changing the niche during ontogeny is greater for species with motile juveniles than for sessile organisms, motility should strongly influence the processes of ecological change. However, the actual implications of sessile life for postlarval changes in ecology are unclear. How do sessile species respond to the changes that occur during juvenile life? Do ecological changes differ in magnitude or in timing between sessile and motile species? What differences exist between sessile and motile species with respect to the way they respond to changes in vulnerability and in energy requirements? Are there other important determinants of the organism's response to changes associated with growth and learning? By addressing these questions, future studies will lead to a better understanding of the link between early juvenile selective pressures and behavioural, physiological, and life history traits.

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