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L. A. Gosselin · F.-S. Chia

# Characterizing temperate rocky shores from the perspective of an early juvenile snail: the main threats to survival of newly hatched *Nucella emarginata*

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**Abstract** Mortality factors most likely to constitute substantial selective pressures for early juvenile gastropods on temperate rocky shores were identified by examining the vulnerability of hatchlings of an intertidal snail, *Nucella emarginata*, to heat stress, desiccation, and predation in 1992 and 1993. The highest temperature of substrata measured at tidal heights colonized by *N. emarginata* in Barkley Sound, British Columbia, Canada, was 28.5 °C. This temperature was not lethal to hatchlings in laboratory tests. In laboratory and field desiccation experiments, all hatchlings died within 6 h of emersion. Early juveniles could not survive direct exposure to even moderate drying conditions for the duration of a low tide. Hence, intertidal microhabitats which dry up even for short periods during low tides would prove lethal. Of 45 intertidal animal species to which hatchlings were exposed in the laboratory, small decapod crustaceans were the only organisms to cause substantial hatchling mortality. Of these, *Pagurus hirsutiusculus* and *Hemigrapsus nudus* were by far the most abundant in the field, and are probably the only important predators of early juvenile *N. emarginata* at most sites. Total predator densities in the field were as high as 438 individuals $m^{-2}$, suggesting that predation pressure may be intense. Desiccation and predation by decapod crustaceans appear to be the most significant threats to early juvenile *N. emarginata*. These factors commonly occur on most temperate rocky shores and undoubtedly constitute major selective agents influencing population parameters and shaping life-history strategies and early juvenile traits of intertidal invertebrates.

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L.A. Gosselin (✉)[1] · F.-S. Chia[1]
Department of Biological Sciences, University of Alberta, Edmonton, Alberta, T6G 2E9, Canada

*Present address*:
[1] Department of Biology, Hong Kong University of Science and Technology, Clear Water Bay, Kowloon, Hong Kong

## Introduction

In benthic marine organisms, the early juvenile period can be a time of considerable mortality (Thorson 1966; Sarver 1979; Jablonski and Lutz 1983; Gosselin and Qian 1995). In fact, mortality during this period can be as important as larval supply in determining recruitment (Osman et al. 1992). Substantial mortality of benthic early juveniles has been reported for macroalgae (Vadas et al. 1990; Brawley and Johnson 1991; Benedetti-Cecchi and Cinelli 1992), barnacles (Denley and Underwood 1979; Young 1991; Gosselin and Qian 1995), bivalves (Bachelet 1989), crabs (Orensanz and Galluci 1988), limpets (Branch 1975), nudibranchs (Sarver 1979), and seastars (Keesing and Halford 1992). Given that a considerable proportion of recruits may die during the early juvenile period, it may be during this period that particular traits and distribution patterns (e.g. colour, shell thickness, behavioural responses to predators, or the distribution of sessile organisms among microhabitats) are established that will characterize populations or local groups of organisms (Gosselin and Qian 1995). Consequently, the main threats to the survival of early juveniles must be identified to understand the significance of larval and juvenile traits, to define the processes controlling recruitment, and to elucidate the significance of early life-history strategies.

The term vulnerability is used here to refer to the likelihood that an organism will die when directly exposed to a given factor or to a specified set of conditions. An organism may be highly vulnerable to a particular factor, however, and yet rarely be killed by it in the field, for example as a result of preferences for microhabitats sheltering it from the influence of the factor. A vulnerability value therefore does not represent the likelihood of the organism being killed in the field. Rather, it indicates how important it is for the organism to avoid exposure to the factor: if an organism is highly vulnerable to a naturally occurring factor,

it will almost certainly be killed unless it can avoid direct exposure to this factor. Hence, vulnerability measurements should be good indicators of the relative importance of individual factors as selective agents.

Intertidal habitats regularly cycle through periods of marine and quasi-terrestrial conditions, exposing their inhabitants to a variety of biotic and abiotic dangers. Accordingly, many factors have been reported to cause mortality of intertidal organisms (Table 1). Although any of these factors may be locally important, predation and desiccation are the most widespread and best-documented mortality factors (e.g. see Underwood 1979). Because vulnerability to predators often decreases with increasing size (Paine 1976; Vermeij 1978, 1993), overall predation risk is highest when individuals are smallest and vulnerable to a broad range of sizes and species of predators (Thorson 1966; Werner and Gilliam 1984). Intertidal organisms are also expected to be most vulnerable to physical factors when they are very small, owing to their high surface to volume ratio (Foster 1971; Vermeij 1972; Wolcott 1973). Few studies, however, have examined the threats to survival of early juveniles in the intertidal zone. In addition, most existing reports only involve sessile organisms, and this information may be of limited relevance to motile organisms.

Early juveniles of many benthic invertebrates are difficult to study due to their small size, sensitivity, sparse distribution, and seasonal availability. Intertidal gastropods, however, are amenable to the study of early juvenile vulnerability because individuals can easily be relocated for laboratory and field experimentation, are relatively undisturbed by gentle handling (Gosselin 1993), and are often abundant and accessible. Consequently, this study aims to characterize temperate

**Table 1** Factors causing mortality of temperate rocky intertidal invertebrates in the field (*Y* yes; *N* no)

| Factor | Organism(s) | Early juveniles? | Sources |
|---|---|---|---|
| Abiotic factors | | | |
| Desiccation | Barnacles | Y | Foster (1971) |
| | Limpets | N | Wolcott (1973) |
| | Limpets | Y | Branch (1975) |
| | Snails | N | Menge (1978) |
| Dislodgement by waves | Mussels | N | Dayton (1971) |
| | Snails | Y | Faller-Fritsch and Emson (1986) |
| | Seastars | N | Menge (1979) |
| Freezing | Bivalves, gastropods, and polychaetes | N | Blegvad (1929) |
| | Mussels | N | Paine (1974) |
| High temperature | Limpets | N | Branch (1975) |
| Ice scouring | Barnacles | N | Wethey (1985) |
| | Barnacles | N | Bergeron and Bourget (1986) |
| Impacts by water-borne debris | Barnacles | Y | Connell (1961) |
| | Mussels and other sessile organisms | N | Dayton (1971) |
| Reduced salinity | Snails | Y | Berry and Hunt (1980) |
| Biotic factors | | | |
| Dislodgement of hummocks | Barnacles on barnacles | N | Barnes and Powell (1950) |
| Dislodgement or ingestion by grazers ("bulldozing") | Snails on barnacles | Y | Petraitis (1983) |
| | Limpets on barnacles | Y | Connell (1961) |
| | Limpets on limpets | Y | Fletcher and Underwood (1987) |
| Immobilization by byssal threads | Mussels on snails | N | Petraitis (1987) |
| Overgrowth, crushing or undercutting by competitors | Barnacles on barnacles | N | Connell (1961) |
| | Algae on barnacles | N | Bertness (1989) |
| | Algae on mussels | N | Dittman and Robles (1991) |
| Algal whiplash | Fucoid algae on barnacles | Y | Southward (1956) |
| Predation | Snails on barnacles | N | Connell (1970) |
| | Snails on mussels | N | Menge (1976) |
| | Seastars on mussels | N | Paine (1976) |
| | Fish and conspecifics on juvenile crabs | N | Fernandez et al. (1993) (see also review by Underwood 1979) |
| Toxic algal blooms | Snails, fishes, and crabs | N | Robertson (1991) |

rocky shores from the perspective of an early juvenile gastropod by identifying mortality factors that are most likely to constitute substantial selective pressures during the early juvenile period. Specifically, we examine the vulnerability of newly hatched *Nucella emarginata* (Deshayes) (northern, cf. Palmer et al. 1990), an intertidal prosobranch gastropod abundant along the rocky shores of northwestern North America, to high temperatures, desiccation, and predation (including the effects of grazers). The prevalence of these factors in the field is also assessed to estimate the importance of these factors for early juvenile survival.

## Materials and methods

### Study site and organism

This study was conducted at the Bamfield Marine Station and at nearby field sites in Barkley Sound, Vancouver Island, Canada (Fig. 1), from May 1992 to September 1993. Ripe egg capsules (unplugged capsules containing metamorphosed individuals that had not yet emerged) were collected at Ross Islets (48°52′35″ N; 125°09′65″ W), Dixon Island (48°51′15″N; 125°06′90″W) and Kirby Point (48°50′85″N; 125°12′40″W). Hatchlings (0.9 to 1.8 mm shell length) that emerged in the laboratory during the first 48 h after collecting the capsules were placed in a separate cage until later use; the age of the hatchlings used in each experiment could therefore be determined with an accuracy of 48 h (time of emergence, $t$, is considered as $t = 0$). Adult *Nucella emarginata* (16 to 26 mm shell length) were collected at Ross Islets (Fig. 1). Individual snails were not used more than once in this study. In Barkley Sound, emersion of substrata at tidal heights colonized by *N. emarginata* lasts 6 to 9 h, depending on tidal amplitude, tidal height, and surface-water conditions (waves).

### Maximum air and seawater temperatures in the field

Since most *Nucella emarginata* in Barkley Sound hatch between May and September (Gosselin 1994), early juveniles may be exposed to high summer temperatures but very few will experience low winter temperatures. Maximum monthly air temperatures for the years 1986 to 1993 were obtained from daily afternoon measurements ≃ 40 m from the shoreline on a property protected from the wind in Grappler Inlet (48°50′05″N; 125°06′90″W (Fig. 1). Maximum monthly summer seawater temperatures for 1986 to 1992 were also obtained from daily measurements (1 m depth) at Cape Beale lighthouse (48°47′20″N; 125°12′95″W), located on the open coast at the southern point of the entrance to Barkley Sound (Fig. 1). Additional maximum seawater temperatures from within Barkley Sound were obtained for June to September of 1991 to 1993 from monthly measurements (10 to 30 cm depth) at Ross Islets, located 10.4 km from Cape Beale.

### Vulnerability to high temperatures

Hatchling vulnerability to high temperatures was examined in controlled laboratory conditions in May 1993. To determine if hatchlings and adults are similarly vulnerable to high temperatures, adult snails were also included in the experiment, although in separate containers. Snails were exposed to temperatures selected as being slightly below (22 °C), close to (26 °C), or slightly higher than (30 °C) the highest they were likely to experience in the field (see "Results –Maximum air and seawater temperatures in the field"). Water temperature in the field and in the laboratory at the time of the experiment was ≃ 11 °C. For each temperature treatment, snails were placed within one of two sub-treatments: (1) emersion: snails were placed in sealed 1.2-liter plastic containers lined with seawater-wetted cloth (5 mm layer) covered with 610 µm-mesh screen to separate the snails from the cloth; (2) immersion: caged snails (95 × 95 × 60 mm cages, with 610 µm-mesh screen) were placed in 20-liter aquaria containing seawater. The emersion treatment provided constant maximum humidity conditions but allowed minimal

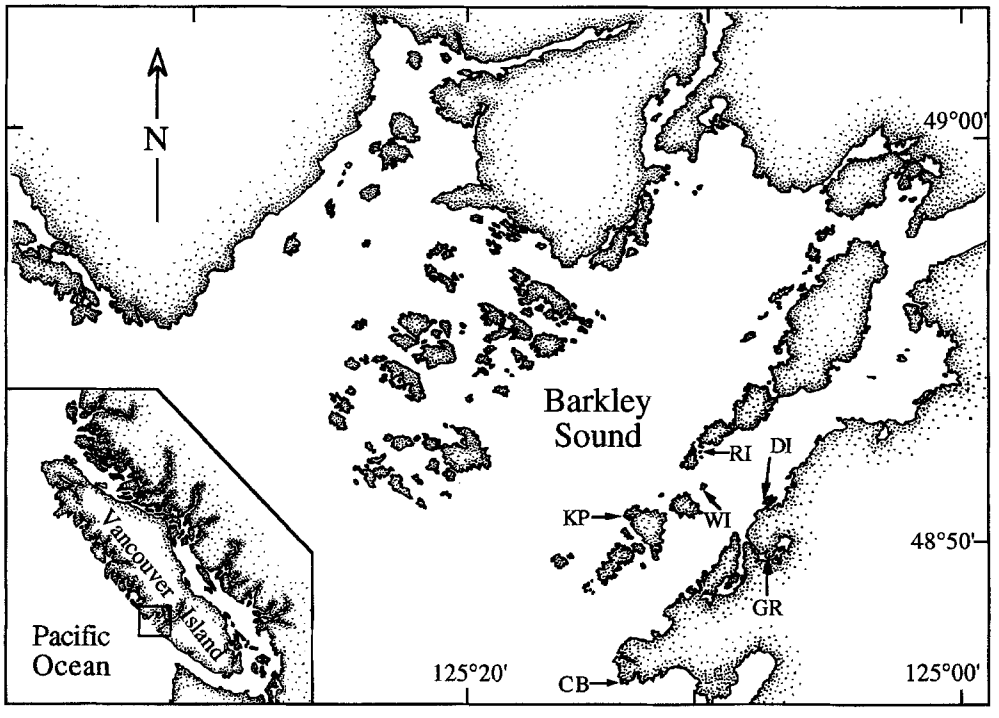


**Fig. 1** Map of Barkley Sound showing study sites (*CB* Cape Beale; *DI* Dixon Island; *GR* Grappler Inlet; *KP* Kirby Point; *RI* Ross Islets; *WI* Wizard Islet)

contact with seawater, simulating field conditions in moist microhabitats, while the immersion treatment simulated conditions in small tidepools that warm during low tide. These sub-treatments also ensured that the effect of temperature would be determined in the absence of desiccation stress. Eight-day old hatchlings and adults were exposed to the following conditions: 22 °C treatment: 8 h in an incubator at 22 °C; 26 °C treatment: 1 h in an incubator at 16 °C, subsequent transfer to a second incubator at 21 °C for 1 h, then to a third incubator at 26 °C for 8 h; 30 °C treatment: 1 h at 18 °C, 1 h at 24 °C, and then 8 h at 30 °C. The intermediate temperatures at the start of the 26 and 30 °C treatments were included to roughly simulate the gradual rise in temperatures of intertidal substrata when the tide recedes. For the immersion sub-treatments, each incubator contained an aquarium with aerated seawater, and only the cages containing snails were transferred from one incubator to the next. At the end of the experiment, all snails were returned to tanks with flowing 11 °C seawater for 12 h, after which each individual was examined under a dissection microscope. Snails not responding when their operculum was touched with a probe were recorded as dead. Hatchlings dying from heat or desiccation (see following subsection) usually had darkened flesh and were easy to recognize.

### Vulnerability to desiccation: laboratory experiment

To determine if newly hatched *Nucella emarginata* can tolerate direct exposure to ambient air for the duration of a low tide, the survival of hatchlings after 6 to 8 h of emersion was assessed. Two-day old hatchlings were placed in an incubator on a shale rock plate (40 × 40 × 3 cm) wetted with seawater. For comparison, adult snails were also placed on a second similar plate in the same incubator. Since evaporation increases with increasing temperature, the experiment was repeated at 15, 22, and 25 °C to simulate a range of conditions likely to occur in the field; 22 °C is reached occasionally during the summer in the intertidal zone in Barkley Sound, while 25 °C occurs infrequently (see "Results – Maximum air and seawater temperatures in the field"). A fan in the incubator maintained a continuous, moderate flow of air throughout the experiment. In each treatment, a separate set of hatchlings and adults were recovered after 1, 2, 4, and 6 h; an additional set was also recovered after 8 h in the 22 °C treatment. Sample sizes for each time interval were as follows: 15 °C: 5 hatchlings and 3 adults; 22 °C: 15 hatchlings and 10 adults; 25 °C: 20 hatchlings and 10 adults. Once removed from the incubator, snails were immediately placed in flowing seawater for 30 min; each individual was then examined for mortality. The period during which snails were left in flowing seawater before being examined for mortality in the high temperature and desiccation experiments ranged from 30 min to 24 h. This is not believed to have affected the results, however, since live snails appeared to recover rapidly, emerging from their shell or even becoming active within 10 to 20 min in flowing seawater (authors' personal observation). Approximate relative humidity was measured with a psychrometer at the start and end of the 22 and 25 °C treatments.

### Vulnerability to desiccation: field experiment

To determine the relevance of laboratory experiments to field conditions, *Nucella emarginata* hatchlings were also exposed to ambient conditions in the intertidal zone at Wizard Islet (48°51′45″N; 125°09′55″W (Fig. 1). Sunny, windy conditions coincided with an afternoon low tide on 11 September 1993, exposing intertidal organisms to high desiccation stress. Hatchlings were brought to the field and placed on three small shale rock plates (8 × 8 × 1 cm). These plates had remained in tanks with flowing seawater for 2 wk prior to this experiment to allow the formation of a biofilm on the surfaces of the plates, as this might affect water retention and snail behaviour. Once in the field, the plates were put in a tray with seawater. Twenty hatchlings (8 to 10 d-old) were placed on each plate. When all hatchlings had attached, the plates were gently removed from the water and placed on a mat ($\simeq 0.75 \times 1$ m) of filamentous algae, *Cladophora columbiana*, growing on an area of flat, horizontal rock. The contact between the plates and the seawater absorbed in the *C. columbiana* mat helped maintain the plates at a temperature similar to the nearby substrata. Tidal height was $\simeq 1.8$ m above mean lower low water (MLLW), a height at which *N. emarginata* snails and egg capsules are commonly found at that site. During the experiment, air temperature and relative humidity were measured 1 cm and 1 m above the plates using an Oakton Model 37200-00 thermohygrometer. Based on the results of the laboratory experiments indicating high mortality during the first 4 h, all hatchlings were recovered after 4 h, returned to the laboratory, and placed in flowing seawater for 24 h. Each individual was then examined for mortality.

### Vulnerability to predators

Intertidal organisms most likely to kill newly hatched *Nucella emarginata* in the field were identified by offering hatchlings to individuals of 45 species. Potential predators were collected from the intertidal at Grappler Inlet (wave-protected), Ross Islets (intermediate wave exposure), and Kirby Point (nearly fully exposed to ocean surge) (Fig. 1). All of these locations supported substantial *N. emarginata* populations. An attempt was made to include most macroscopic intertidal grazers and predatory species that may co-occur with *N. emarginata* in the field. Grazers were included as potential predators because they can crush or ingest early juvenile barnacles (Connell 1961; Miller and Carefoot 1989), ascidians (Young and Chia 1984), and limpets (Fletcher and Underwood 1987) and thus may also be a threat to very small snails. Three to six individuals of each potential predator species were collected. Each individual was separately placed in a cage without food for 2 to 3 d. Ten hatchlings were then added to each cage. The contents of each cage were examined after 3 d. Cage sizes were large cages = 95 × 95 × 60 mm, and small cages = 39 mm diameter × 62 mm long, the latter being used for small potential predators.

### Predator densities in the field

To determine the abundance of predators in the field, densities of the most common species that killed hatchlings in the laboratory (3 hermit crabs and 1 shore crab) were assessed at three sites between 16 August and 7 September 1993, a time of year when hatchling and juvenile *Nucella emarginata* are generally abundant. Ross Islets, Wizard Islet, and Dixon Island sites (low-moderate, moderate, and moderate-high exposure to wave action, respectively) had previously been noted as supporting substantial densities of hermit crabs and shore crabs (authors' personal observation). At each site, five quadrats (25 × 25 cm) were sampled at 1 m intervals along each of two 5 m transects running parallel to the shore at 1.2 to 1.8 m above MLLW (10 quadrats per site).

## Results

### Maximum air and seawater temperatures in the field

Air temperatures in Grappler Inlet remained below 30 °C in 4 of 8 yr (1986–1993, Fig. 2a), and equalled or slightly exceeded 30 °C only on a few occasions in the other four years. The highest air temperature recorded

over the 8 yr period was 31.5 °C (July 1991). Air temperatures > 26 °C occurred only on a few days each summer, and these did not often coincide with afternoon low tides. Moreover, air temperatures in the intertidal zone in Barkley Sound on warm days were ≃ 4 to 8 C° cooler than at the site where temperatures were recorded in Grappler Inlet (authors' personal observation). Thus, air temperature at low tide in the intertidal zone is unlikely to exceed 26° C, and was not observed to exceed 24 °C during four summers of field work (1990–1993).

Seawater temperatures on the exposed coast did not exceed 18° C between 1986 and 1992 (Cape Beale, Fig. 2b). Surface waters became warmer within Barkley Sound than on the open coast during the summer, but did not exceed 20 ° C over a 3 yr period (Ross Islets, Fig. 2b).

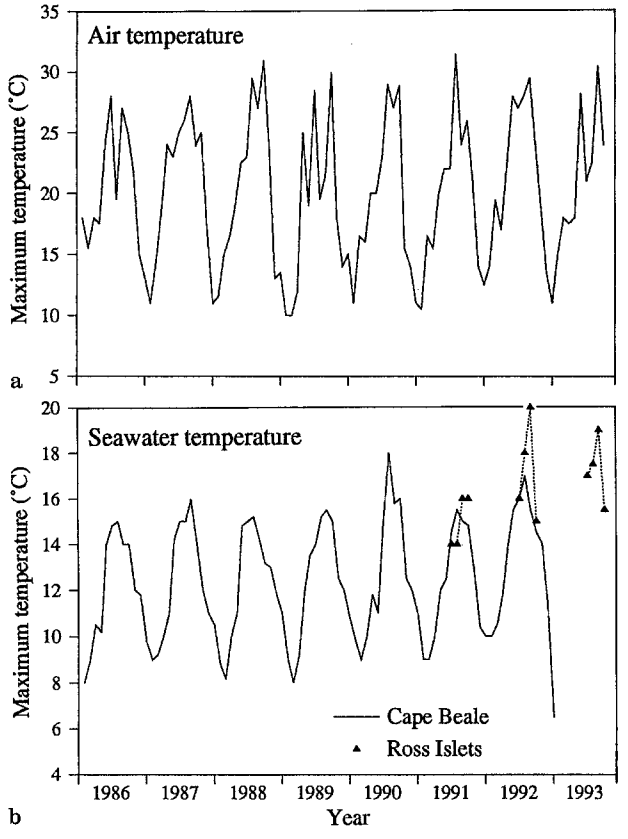


**Fig. 2** Maximum monthly temperatures recorded in Barkley Sound from 1986 to 1993. **a** Maximum air temperatures in Grappler Inlet; **b** maximum surface seawater temperatures at Cape Beale (1 m depth) and Ross Islets (10 to 30 cm depth)

## Vulnerability to high temperatures

*Nucella emarginata* hatchlings were not vulnerable to temperatures as high as 26 °C, as all hatchlings survived 8 h at 22 and 26 °C (Table 2). Hatchling mortality did occur, however, at 30 °C. At this temperature, most hatchlings in the emersion sub-treatment died. Only one death was recorded among hatchlings immersed in 30 °C seawater. Hence, during low-tide emersion, temperatures of ≃ 30 °C or higher could be lethal for hatchlings from Barkley Sound populations. Adults, however, survived well in all temperature treatments (Table 2).

## Vulnerability to desiccation: laboratory experiment

No hatchling survived 6 h of emersion at any of the three temperatures used in this study (Fig. 3). Survival time decreased with increasing temperature. At 25 °C, all hatchlings were dead within 2 h. Relative humidity within the incubator was 22 °C treatment: initial = 86%, 6 h = 80%, 8 h = 77%; 25 °C treatment: initial = 84%, 6 h = 66%. No humidity measurements were taken during the 15 °C treatment. Adult snails had 100% survival throughout all laboratory desiccation experiments.

## Vulnerability to desiccation: field experiment

All 20 hatchlings on each of the three plates set in the intertidal zone at Wizard Islet died during the 4 h of direct exposure to low-tide conditions. Relative humidity at 1 cm above the plates (Table 3) was comparable to the measurements obtained in the laboratory experiments. These mortality results are in agreement with those obtained in the laboratory experiments, indicating that hatchling *Nucella emarginata* are not likely to

**Table 2** *Nucella emarginata*. Mortality of hatchlings and adults (16 to 25 mm shell length) after 8 h in different temperature treatments. Values represent average mortality rate (%) ± SD, each based on three replicates. Replicates consisted of 8 hatchlings or 4 adults

| | 22 °C | | 26 °C | | 30 °C | |
|---|---|---|---|---|---|---|
| | emersion[a] | immersion[b] | emersion | immersion | emersion | immersion |
| Hatchlings | 0 ± 0 | 0 ± 0 | 0 ± 0 | 0 ± 0 | 83.3 ± 14.4 | 4.2 ± 7.2 |
| Adults | 0 ± 0 | 0 ± 0 | 0 ± 0 | 8.3 ± 14.4 | 0 ± 0 | 0 ± 0 |

[a] Emersion sub-treatment: snails were placed in sealed containers maintaining constant maximum humidity
[b] Immersion sub-treatment: snails were kept immersed in seawater

survive > 4 h of direct exposure to drying conditions occurring in the field at low tide.

## Vulnerability to predators

Of the 45 species of intertidal invertebrates that were placed in cages with hatchlings, only decapod crustaceans and one fish species caused hatchling mortality (Table 4). Decapod predators crushed hatchlings, leaving only shell fragments. In separate tests, large *Hemigrapsus nudus* ( ≥ 29.5 mm carapace width, CW) or *Cancer productus* ( ≥ 30 mm CW) would not attack hatchlings. Small *Gobiesox maeandricus* (body length, BL ≤ 47 mm), an intertidal fish, swallowed some hatchlings over the 3 d period; most of the ingested hatchlings were found alive in translucent fecal sacs, but these hatchlings did not escape from the sacs and died after a few days. Hatchling mortality in cages with other species was similar to that observed in the controls. For *Pisaster ochraceus* (Table 4), all mortality (four hatchlings) occurred in the cage with the smallest seastar (radial length, R = 9.8 mm).

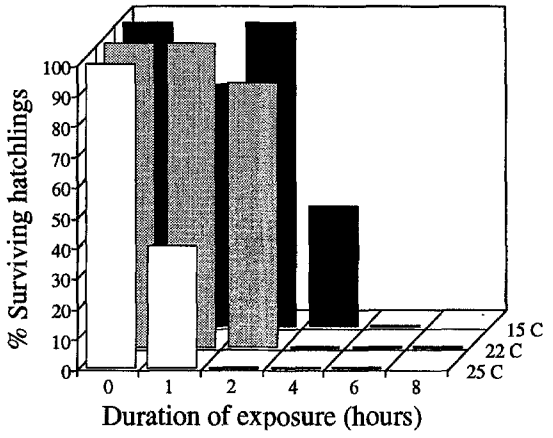


**Fig. 3** *Nucella emarginata.* Survival time of newly hatched individuals when emersed for up to 6 h (15, 25°C) or 8 h (22°C). Hatchlings were then placed in flowing seawater for 30 min before being examined for mortality. Each value represents survival of a separate set of 5 (15°C), 15 (22°C) or 20 (25°C) hatchlings

## Predator densities in the field

Of the species that consumed hatchlings in the laboratory (Table 4), all but four were infrequently observed in areas inhabited by *Nucella emarginata.* However, the total density of hermit crabs (*Pagurus hirsutiusculus, P. granosimanus,* and *P. samuelis*) and shore crabs (*Hemigrapsus nudus*) exceeded 400 individuals $m^{-2}$ at Ross Islets, the most protected of the three sites (Table 5). Densities of both *P. hirsutiusculus* and *H. nudus* were consistently high at all three sites. Densities of *H. nudus* as high as 360 individuals $m^{-2}$ were also observed on a nearby islet at Ross Islets in June 1988 (Rawlings 1990). Our observations at several other local sites confirmed that these two predators were abundant at almost all sites and could even be found among *Mytilus californianus* beds and in tide pools on the open coast. In fact, these results (Table 5) probably underestimate actual densities since many hermit crabs were in tidepools during low tides and only a few small tidepools were sampled during this study. As the rising tide immersed the intertidal, an army of hermit crabs could be seen emerging from tidepools and moist habitats to forage. Other decapods readily consuming hatchlings in the laboratory were generally found at very low densities in areas populated by *N. emarginata.* The intertidal fish *Gobiesox maeandricus* and small individuals of the seastar *Pisaster ochraceus* (R ≤ 40 mm) were almost exclusively found under rocks and boulders in the low intertidal, such that their distribution rarely overlapped with that of *N. emarginata.* The distribution of *G. maeandricus* at high tide, however, is not known.

**Table 3** Temperature and relative humidity measured above experimental rock plates at Wizard Islet on 11 September 1993 during field desiccation experiment. Measurements were carried out at low tide at ≃ 1.8 m above mean lower low water. Experimental area had been emersed for ≃ 2.5 h when first temperature and humidity measurements were made. Values are means ± SD; number of measurements in parentheses

| Height above plates | Time of measurement (hrs) | | | |
|---|---|---|---|---|
| | 14:30 | 15:30 | 16:30 | 17:30 |
| Air temperature (°C) | | | | |
| 1 cm | 16.8 (1) | 17.8 ± 0.4 (3) | 16.8 ± 0.0 (3) | 15.5 ± 0.4 (3) |
| 1 m | 16.4 (1) | 16.2 (1) | 16.9 (1) | 15.3 (1) |
| Relative humidity (%) | | | | |
| 1 cm | 78.2 (1) | 74.6 ± 3.3 (3) | 77.4 ± 1.8 (3) | 81.6 ± 2.7 (3) |
| 1 m | 70.5 (1) | 63.0 (1) | 69.9 (1) | 73.4 (1) |

**Table 4** Identification of intertidal predators of newly hatched *Nucella emarginata*. Replicate cages contained one individual potential predator and 10 hatchlings for 3 d. Control cages contained only hatchlings. Classification of invertebrates is based on Kozloff (1987) (*BD* body diameter; *BL* body length; *CL* claw length; *CW* carapace width; *R* radial length; *SD* shell diameter; *SL* shell length; *n* number of replicates)

| Potential predator species | Size range (mm) used in experiments | (*n*) | Dead or missing hatchlings ($\bar{x} \pm$ SD) |
|---|---|---|---|
| Controls | | (2) | $0.5 \pm 0.7$ |
| Cnidaria | | | |
| Anthozoa | | | |
| *Anthopleura elegantissima* | 7.9–28.5 BD | (3) | $1.0 \pm 1.0$ |
| Annelida | | | |
| Polychaeta | | | |
| *Nereis vexillosa* | 33–150 BL | (5) | $0 \pm 0$ |
| Mollusca | | | |
| Gastropoda | | | |
| Prosobranchia | | | |
| Archaeogastropoda | | | |
| Patellacea | | | |
| *Lottia digitalis* | 7.7–13.5 SD | (3) | $0 \pm 0$ |
| *Lottia pelta* | 5.8–23.8 SD | (3) | $0 \pm 0$ |
| Trochacea | | | |
| *Calliostoma ligatum* | 6.5–18.9 SD | (3) | $0.3 \pm 0.6$ |
| *Tegula funebralis* | 9.6–15.5 SD | (3) | $0 \pm 0$ |
| Mesogastropoda | | | |
| *Littorina scutulata* | 4.8–9.5 SL | (3) | $0 \pm 0$ |
| *Littorina sitkana* | 3.9–10.3 SD | (3) | $0 \pm 0$ |
| *Bittium eschrichtii* | 5.0–11.7 SL | (5) | $0.8 \pm 1.3$ |
| Neogastropoda | | | |
| Muricacea | | | |
| *Ceratostoma foliatum* | 12.4–39.6 SL | (3) | $0 \pm 0$ |
| *Ocenebra lurida* | 3.7–13.3 SL | (3) | $0.3 \pm 0.6$ |
| *Nucella canaliculata* | 6.7–26.7 SL | (3) | $0 \pm 0$ |
| *Nucella emarginata* | 18.2–26.0 SL | (3) | $0 \pm 0$ |
| *Nucella lamellosa* | 18.5–26.0 SL | (3) | $0 \pm 0$ |
| Buccinacae | | | |
| *Lirabuccinum (Searlesia) dira* | 10.7–32.6 SL | (6) | $0.3 \pm 0.5$ |
| *Alia (Mitrella) gouldi* | 4.5–9.5 SL | (3) | $0.3 \pm 0.6$ |
| *Amphissa columbiana* | 6.8–22.4 SL | (3) | $0.7 \pm 1.2$ |
| Opisthobranchia | | | |
| Pyramidellacea | | | |
| *Odostomia* sp. | 3.7–6.0 SL | (5) | $0 \pm 0$ |
| Nudibranchia | | | |
| *Aeolidia papillosa* | 9.1–36.2 BL | (3) | $0 \pm 0$ |
| *Archidoris montereyensis* | 24.3–34.8 BL | (3) | $0 \pm 0$ |
| Gymnomorpha | | | |
| *Onchidella borealis* | 5.1–8.9 BL | (3) | $0 \pm 0$ |
| Arthropoda | | | |
| Crustacea | | | |
| Isopoda | | | |
| *Cirolana harfordi* | 4.3–20.4 BL | (3) | $0 \pm 0$ |
| *Gnorimosphaeroma oregonense* | 2.7–3.5 BL | (3) | $0 \pm 0$ |
| *Idotea wosnesenskii* | 16.1–32.5 BL | (5) | $0 \pm 0$ |
| Amphipoda | | | |
| *Hyale pugettensis* | 7.5–12.9 BL | (3) | $0 \pm 0$ |
| Decapoda | | | |
| *Pagurus granosimanus* | 2.9–8.4 CL | (5) | $5.8 \pm 4.1$ |
| *Pagurus hemphili* | 5.7–8.5 CL | (3) | $7.3 \pm 2.1$ |
| *Pagurus hirsutiusculus* | 4.7–9.4 CL | (3) | $9.3 \pm 1.2$ |
| *Pagurus samuelis* | 4.5–5.9 CL | (3) | $9.3 \pm 1.2$ |
| *Oedignathus inermis* | 6.9–12.3 CW | (3) | $9.6 \pm 0.6$ |
| *Pachycheles pubescens* | 5.5–13.4 CW | (3) | $0 \pm 0$ |
| *Petrolisthes cinctipes* | 5.6–13.5 CW | (3) | $0 \pm 0$ |
| *Pugettia producta* | 5.2–13.2 CW | (3) | $1.0 \pm 0.0$ |
| *Pugettia richii* | 10.2–15.9 CW | (3) | $8.6 \pm 2.3$ |
| *Cancer productus* | 16.5–26.4 CW | (4) | $8.8 \pm 1.3$ |
| *Cancer oregonensis* | 13.6–24.7 CW | (3) | $8.6 \pm 1.5$ |
| *Hemigrapsus nudus* | 7.7–13.5 CW | (5) | $7.0 \pm 3.3$ |

(continued overleaf)

**Table 4** (continued)

| Potential predator species | Size range (mm) used in experiments | (*n*) | Dead or missing hatchlings ($\bar{x} \pm$ SD) |
|---|---|---|---|
| Echinodermata | | | |
| Asteroidea | | | |
| *Dermasterias imbricata* | 14.1–26.6 R | (3) | $0 \pm 0$ |
| *Henricia leviuscula* | 7.4–18.1 R | (3) | $0 \pm 0$ |
| *Leptasterias hexactis* | 10.0–29.5 R | (5) | $0.8 \pm 0.8$ |
| *Pisaster ochraceus* | 9.8–20.0 R | (4) | $1.5 \pm 1.7$ |
| Holothuroidea | | | |
| *Cucumaria pseudocurata* | 13.5–26.5 BL | (4) | $0 \pm 0$ |
| Chordata | | | |
| Pisces (intertidal fish) | | | |
| *Anoplarchus purpurescens* | 54–84 BL | (3) | $0 \pm 0$ |
| *Gobiesox maeandricus* | 39–88 BL | (5) | $3.2 \pm 2.6$ |
| *Oligocottus maculosus* | 21–44 BL | (3) | $0 \pm 0$ |

**Table 5** Densities (average nos. $m^{-2} \pm$ SD) of four main predators of *Nucella emarginata* hatchlings at three field sites. At each site, 10 quadrats (25 × 25 cm) were sampled along two 5 m transects set parallel to shore. The listed densities were obtained from counts of predators ≥ the smallest predator capable of killing a 1.2 mm hatchling. The smallest predator sizes, determined using regression equations between predator claw length (CL) and largest snail killed (authors' unpublished data), were: *H. nudus*: 2.76 mm CL; *P. hirsutiusculus*: 2.31 mm CL; *P. granosimanus*: 2.03 mm CL; *P. samuelis*: 2.31 mm CL

| Predator species | Ross Islets | Wizard Islet | Dixon Island |
|---|---|---|---|
| *Hemigrapsus nudus* | $171.2 \pm 215.9$ | $67.2 \pm 98.9$ | $41.6 \pm 42.8$ |
| *Pagurus hirsutiusculus* | $225.6 \pm 279.0$ | $203.2 \pm 172.5$ | $107.2 \pm 59.9$ |
| *P. granosimanus* | $30.4 \pm 57.7$ | $8.0 \pm 20.31$ | $0.0 \pm 0.0$ |
| *P. samuelis* | $11.2 \pm 26.2$ | $1.6 \pm 5.1$ | $19.2 \pm 36.0$ |
| Total *Pagurus* spp. | $267.2 \pm 350.6$ | $212.8 \pm 184.5$ | $126.4 \pm 85.2$ |
| Total predators | $438.4 \pm 498.3$ | $280.0 \pm 242.9$ | $168.0 \pm 89.0$ |

## Discussion

### Vulnerability to high temperatures

Although most *Nucella emarginata* in Barkley Sound hatch during the summer, when air and surface seawater temperatures are highest, the results of the present study suggest that high temperatures are not likely to be an important direct cause of early juvenile mortality.

Hatchlings located in moist microhabitats could survive the duration of a low tide at temperatures of at least 26 °C (Table 2), and some hatchlings could even survive at 30 °C. It is probable that most would survive short durations at temperatures of 28 to 30 °C. Air temperatures in Barkley Sound rarely reach 24 °C, and possibly never exceed 26 °C. Although intertidal substrata exposed to sunlight can become warmer than air, the highest temperatures will only occur for a short time towards the end of the low-tide period, and may never exceed 30° C in Barkley Sound. On 4 August 1993, the warmest day of the year (30.5° C in Grappler Inlet, only 1C° cooler than the warmest temperature recorded between 1986 and 1993), air temperature 10 cm above mid-intertidal substrata at Dixon Island only reached 24 °C. Dry rock surfaces exposed to the sun at ≃ 2.1 m above MLLW, near the upper limit of *Nucella emarginata* distribution at that site, reached 28.5 °C at 12:30 hrs (≃ 30 min before being immersed by the incoming tide). At that time, the temperature of shaded rock surfaces only reached 22 °C.

Surface seawater temperature never exceeded 20 °C and is probably not a direct cause of mortality in Barkley Sound, as most hatchlings and adults can survive at least 8 h of immersion in seawater at 30 °C.

Previous studies of late juvenile or adult invertebrates have concluded that maximum temperatures on temperate rocky shores were below lethal levels (Davies 1969; Wolcott 1973; Underwood 1979). The present study suggests that the same is true for early juveniles, even though early juveniles may be more vulnerable than adults. High temperatures may nevertheless be an indirect cause of mortality by increasing evaporation rates (Wolcott 1973), and thus mortality by desiccation.

### Vulnerability to desiccation

Early juvenile *Nucella emarginata* are not likely to survive direct exposure to even moderate drying conditions for the duration of a low tide. In both laboratory and field desiccation experiments, hatchlings started dying shortly after the substratum dried, and no hatchling survived 6 h of emersion. The absence of mortality in the 26 ° C treatment of the high-temperature experiment confirms that mortality in the desiccation experiments was indeed caused by desiccation rather than heat stress. Microhabitats that dry out even for short periods during low tides would thus prove lethal. But while desiccation conditions in the field can be a serious threat to early juveniles, they will rarely be lethal for healthy adults. Vulnerability to desiccation also decreases with increasing size in barnacles (Foster 1971), limpets (Wolcott 1973; Branch 1975), seastars (Menge 1972), and other snails (Berry and Hunt 1980; Garrity 1984).

Relative humidity in the intertidal zone probably remains higher at the surface of intertidal substrata than in surrounding air (Table 3). Nevertheless, near-surface humidity levels, in combination with air circulation, are low enough to produce substantial desiccation of intertidal substrata and organisms, as was often evidenced by the dry, brittle fronds of macroalgae at low tide. Humidity levels at the surface of mid-intertidal substrata in Barkley Sound can reach levels that would result in 100% mortality of exposed hatchling *Nucella emarginata*.

## Vulnerability to predators

Contrary to the suggestion by Thorson (1966) that small juvenile invertebrates will be preyed upon by a wide variety of predators, few species killed newly hatched *Nucella emarginata*. Laboratory experiments suggest that decapod crustaceans are the only important predators of hatchlings in Barkley Sound. These species, however, are abundant and could exact a heavy toll on young cohorts.

Decapod predators do consume hatchlings in the field, as shell fragments are regularly found in samples of filamentous algae and mussel clusters (authors' personal observation). Hermit crabs, especially *Pagurus hirsutiusculus*, are active foragers and are often active even at low tide until the surfaces dry out. In addition, they were often observed "sitting" on clutches of ripe egg capsules, possibly feeding on the young snails as they emerged from the capsules. In the laboratory, *P. hirsutiusculus* rapidly finds and consumes all *Nucella emarginata* hatchlings (present study), and will also feed on hatchlings of a variety of other gastropod species (Spight 1976; Rivest 1983). It is often the most abundant and is probably the most important predator of early juvenile *N. emarginata* and other small gastropods at most field sites.

According to Knudsen (1964), *Hemigrapsus nudus* feeds mainly on plant material and occasionally consumes animal tissue. *H. nudus* will, however, feed on littorines (Boulding and Van Alstyne 1993) and on *Nucella emarginata* egg capsules in the field (Rawlings 1990). Although hatchlings are probably not a preferred food item of *H. nudus*, this predator may nevertheless be responsible for a significant portion of hatchling mortality, given its high densities among habitats colonized by *N. emarginata*.

None of the grazers or other herbivores caused hatchling mortality. Birds, which were reported to consume small *Nucella lapillus* on British shores (Feare 1970), were not observed feeding on *N. emarginata*. Levels of predation by pelagic fish are unknown.

Hatchling and adult *Nucella emarginata* have distinct sets of predators. In separate trials (authors' unpublished data), the largest *Pagurus hirsutiusculus* (claw length, CL = 14.0 mm) never killed or damaged adult snails. The largest *Hemigrapsus nudus* to attack snails (CL = 21.1 mm) could kill small adults ($\leq$ 17 mm shell length), but this was infrequent even when crabs and snails were confined to the same cage for several days, and such large *H. nudus* have not been observed in *N. emarginata* habitats. Predators of adult *N. emarginata*, large *Pisaster ochraceus* (R $\gtrsim$ 40 mm) and *Cancer productus* (CW $\gtrsim$ 40 mm), never killed hatchlings.

Shell-crushing predators have been identified as selective agents influencing the morphology of gastropod shells (Vermeij 1978, 1987, 1993; Crothers 1985; Palmer 1985; Faller-Fritsch and Emson 1986). The results of the present study show that shell-crushing predators can be the only predators of gastropods at the onset of independent benthic life. For *Nucella emarginata*, predators that do not damage the shell, such as seastars, become important later in life. Structural features that increase resistance to shell-crushing predators could therefore have a greater effect on survival during the vulnerable early juvenile period than at any time later in life. Yet, shell spines, ribs, varices, and teeth are usually absent or minimal in very young snails, but are most developed in mature individuals (Vermeij 1987, 1993). Rapid growth is often considered to be an important strategy used by young organisms to reduce mortality due to predation (Werner and Gilliam 1984; Vermeij 1987). Growth, however, does not solve the immediate problem of high vulnerability. Other features such as initial shell size, shape, and thickness could be important elements of the adaptive response of early juveniles to predators (Spight 1976; Rivest 1983). Nevertheless, all newly-hatched *N. emarginata* remain vulnerable to abundant predators and to low-tide desiccation conditions; use of microhabitats which offer protection from these mortality factors may be an important means of surviving through the early juvenile period (Gosselin 1994).

## Other factors

Other potential causes of mortality include dislodgement by waves and crushing by water-borne debris. In laboratory observations (authors' unpublished data), hatchlings were able to remain attached and even crawl on a rock surface when exposed to moderately high levels of turbulence (flow velocities up to $\simeq$ 15 cm $s^{-1}$). Consequently, waves and water currents might cause little mortality on protected or moderately wave-exposed shores. However, dislodgement by waves could be important at sites exposed to strong wave action. Hatchling *Nucella emarginata* are probably most vulnerable to dislodgement when they emerge and crawl off their egg capsule, which is flexible and may provide poor footing in turbulent conditions. They were never observed emerging at low tide, however, and were infrequently found on or at the base of the egg capsules when the tide was out. This suggests that individuals within the capsules may be able to

recognize conditions that indicate the tide is receding and stop emerging some time before the capsule is exposed.

During laboratory experiments (Gosselin and Chia 1994), $\simeq 15\%$ of newly hatched *Nucella emarginata* died of unknown causes during the first 30 d after hatching; these snails had been continuously immersed in flowing seawater, provided with food, and no predators were present. Under similar conditions, 69.6% of recently hatched *Searlesia dira*, a prosobranch gastropod, died over a period of 36 d (Rivest 1983). Diseases, parasites, damage due to ultraviolet radiation, and complications during metamorphosis may cause substantial early juvenile mortality. Little information is available on the occurrence of these factors in intertidal organisms.

## Conclusion

Desiccation and predation by decapod crustaceans (*Pagurus* spp. and *Hemigrapsus nudus*) appear to be the most significant threats to early juvenile *Nucella emarginata*. At sites exposed to intense wave action, dislodgement by waves may also become an important factor. These factors, particularly desiccation, are prevalent on most temperate rocky intertidal shores. When intertidal invertebrates with motile early juveniles hatch or settle and begin to explore their new habitat, they are directly exposed to these factors. In newly hatched *N. emarginata*, these factors can rapidly cause 100% mortality of early juveniles that are not protected from their effects. Consequently, desiccation and predation by decapod predators undoubtedly exert considerable selective pressures on intertidal invertebrate populations, shaping life-history strategies and early juvenile traits, such as timing of settlement or hatching relative to the tidal cycle and microhabitat preferences.

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