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Predation on juveniles of *Crepidula fornicata* by two crustaceans and two gastropods

Jan A. Pechenik *, Olivia V. Ambrogio, Steven Untersee

Biology Department, Tufts University, Medford, MA 02155, USA

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ABSTRACT

Crepidula fornicata, the slippershell snail, while native to New England, has now become a successful invasive species along coastlines in many other parts of the world. This study considers the possible control of native populations by several common predators: the invasive shore crab *Hemigrapsus sanguineus*, one species of pagurid hermit crab (*Pagurus longicarpus*), and juveniles of the drilling gastropods *Nucella lapillus* and *Urosalpinx cinerea*. In the laboratory, juveniles of *C. fornicata* were especially vulnerable to the two crustacean predators tested, and to a lesser extent vulnerable as well to predation by the oyster drill *U. cinerea*; in choice tests, young oyster drills ate barnacles and mussels rather than slippershell snails, but ate *C. fornicata* when offered no other choice. Juveniles of two other *Crepidula* species (*C. plana and C. convexa*) were less susceptible to predation by hermit crabs, probably due to differences in juvenile shell morphology and growth trajectories. Remarkably, juvenile dogwhelks (*N. lapillus*) ate no *Crepidula* prey over several months in the laboratory, even in the absence of alternative food and although they readily consumed blue mussels. Additional work is needed to determine the role of crustacean and other predators in regulating the growth of native populations of *C. fornicata* in the field and to determine the extent to which the explosive growth of at least some invasive *Crepidula* populations reflects escape of juveniles from native predators.

1. Introduction

Over the past 50 years, *Crepidula fornicata*, a suspension-feeding marine gastropod native to the North American Atlantic coast, has become invasive on the west coast of the U.S. and along the coastlines of Asia, Europe, and Scandinavia (reviewed by Blanchard 1997; Thieltges et al., 2004). The Brittany coast of France now supports some especially large populations of *C. fornicata* (Blanchard, 1997, Blanchard, 2009; Ehrhold et al. 1998; Thieltges et al., 2004), causing substantial habitat modification (e.g., Thieltges et al., 2003), adverse effects on fisheries (Blanchard, 1997, 2009; Le Pape et al., 2004), and various other ecological effects (Decottignies et al., 2006; Leloup et al., 2008; de Montaudouin and Sauriau, 1999; Le Pape et al., 2004; Thieltges et al., 2006; reviewed by Valdizan et al., 2009). The *C. fornicata* population increased substantially between 1996 and 2004 in one of the best-studied areas, the Bay of Mt. Saint-Michel, with biomass rising from an estimated 107,475 metric tons to nearly 150,000 metric tons (Blanchard, 2009), an increase of over 5 thousand metric tons per year.

The reasons for *C. fornicata*'s extraordinary success in many of the areas into which it has been introduced are still unknown. One factor that often influences the success of invasive species is the release of those species from predation pressure in the new environment (Schoener and Spiller, 1995; Owen and Lewis, 2001; Wolfe 2002; Kotiaho and Sulkava, 2007). However, little work has been done to identify the predators of *C. fornicata* even in its native habitat; the few existing studies have shown that, in their native habitat, adults of *C. fornicata* are preyed on by oyster drills (*Urosalpinx cineraria* [Pratt, 1974a]), juvenile tautog fish (Clark et al., 2006), and possibly some seastars (*Asterias*), crabs (*Cancer borealis*), and polychaetes (Hoagland, 1974). In some laboratory studies, adult shore crabs (*Carcinus maenas*) and seastars (*Asterias rubens*) largely ignored *C. fornicata* over a wide range of sizes and fed instead on the mussel *Mytilus edulis* (Thieltges et al., 2004). In contrast, in another study the seastar *Asterias forbesi* preyed more heavily on *C. fornicata* than on the oyster *Crassostrea virginica* (Reichert and Sclafani, 2008).

These previous studies have considered only predation on large (>1 cm) individuals of *C. fornicata*. However, predation is often heaviest on young, newly metamorphosed juveniles (reviewed by Walters and Wethey, 1996; Gosselin and Qian, 1997; Hunt and Scheibling, 1997), with juvenile populations commonly being reduced by 80% within the first 4 months after recruitment (reviewed by Gosselin and Qian, 1997). In some cases, more than 30% of juveniles have died within 24 h of metamorphosing (e.g., the barnacle *Balanus glandula*; Gosselin and Qian 1997). Thus, predation on recently metamorphosed juveniles can strongly influence the size and density of adult populations. If we are interested in identifying the types and extent of predation on a species – especially on a species whose success as an invader may be related to its release from predators – then identifying the species that prey on juveniles and the strength of the predation pressure they exert on those juveniles is particularly important.

* Corresponding author. Present address: Biology Department, Tufts University, Medford, MA 02155, USA. Tel.: +1 617 627 3199.
E-mail address: jan.pechenik@tufts.edu (J.A. Pechenik).

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Females of *C. fornicata* release feeding larvae into the plankton (Werner, 1955; Calabrese and Rhodes, 1974; Pechenik, 1980). The larvae have shell lengths of about 1 mm when they first become competent to metamorphose (Pechenik and Heyman, 1987; Pechenik and Gee, 1993). Following metamorphosis, juveniles of *C. fornicata* grow rapidly, typically between about 100 and 200 μm day^{-1} in the laboratory (Pechenik and Eyster, 1989; Pechenik et al., 1996a, b).

In this study we looked at the size-specific vulnerability of *C. fornicata* juveniles (initial shell lengths <1 cm) to 4 potential predators that are abundant intertidally in their native habitat: the hermit crab *Pagurus longicarpus*; the invasive shore crab *Hemigrapsus sanguineus*; and the inexperienced juveniles of 2 carnivorous snails, the oyster drill *Urosalpinx cinerea* and the dogwhelk *Nucella lapillus*. We used juvenile snail predators in these experiments, obtained from laboratory hatchings, because prey preference is known to be affected by prior experience in these and related species (e.g., Wood, 1968; Hughes and de Dunkin, 1984; Palmer, 1984; Gosselin and Chia, 1996).

In addition, because hermit crabs turned out to be particularly effective predators of juvenile *C. fornicata*, we examined the vulnerability of the juveniles of 2 congeneric species, *Crepidula convexa* and *C. plana*, to the same hermit crab predator. *C. convexa* and *C. plana* co-occur with *C. fornicata* in its native habitat but differ from *C. fornicata* considerably in shell morphology (especially true for *C. plana*, true to a lesser extent for *C. convexa*) or juvenile growth rate (*C. convexa*). As with *C. fornicata*, *C. plana* releases swimming larvae that metamorphose to the juvenile stage at shell lengths of about 1 mm (Lima and Pechenik, 1985). In contrast, *C. convexa* lacks a free-living juvenile stage: juveniles emerge from incubated egg capsules into the benthos at shell lengths of approximately 1 mm (Hendler and Franz, 1971; Li and Pechenik, 2007).

2. Materials and methods

2.1. Animal collection and care

The experiments were conducted over 4 years (2001–2005), as indicated below. All studies were conducted using artificial seawater (Instant Ocean, approximately 30 psu), filtered to 1 μm before use. In some experiments, predators were given a choice of prey – the mussel *M. edulis* or the barnacle *Semibalanus balanoides* – in addition to one of the 3 *Crepidula* species of primary interest. The crustaceans, mussels, and barnacles used in these experiments were collected intertidally at Nahant, MA, Fairhaven, MA, or Bissel Cove, RI and held in the laboratory in glass jars in 1 μm-filtered seawater at ~22 °C with constant aeration. The predatory gastropods *N. lapillus* and *U. cinerea* were collected from the same locations, but as encapsulated embryos so that the young predators would have had no prior experience feeding on any particular prey species when the experiments began. When juvenile predators emerged from the egg capsules in the laboratory, they were transferred to small plastic cages with mesh sides (see below), so that they would remain submerged in the aerated seawater until they were used in experiments. Experiments with *N. lapillus* were conducted in 2001–2002, while experiments with *U. cinerea* were conducted in 2005.

To obtain juveniles of the gastropods *C. fornicata* and *C. plana*, adults were collected at the above locations and larvae were reared through metamorphosis in the laboratory using standard techniques (e.g., Blanchard et al., 2008; Lima and Pechenik, 1985; Pechenik, 1984; Pechenik and Lima, 1984; Pechenik and Gee, 1993). Following metamorphosis (induced by exposure to 20 mM excess KCl—Pechenik and Heyman, 1987; Eyster and Pechenik, 1988; Pechenik and Gee, 1993), juveniles were kept in the same conditions as the other potential prey. Mussels, barnacles, and juvenile *Crepidula* spp. were all fed daily with the naked flagellate *Isochrysis galbana* (clone T-ISO); all of these animals are suspension-feeders. Using excess KCl to induce metamorphosis of *C. fornicata* does not affect juvenile survival or growth rate (Eyster and Pechenik, 1988).

2.2. N. lapillus as a potential predator of C. fornicata

Newly hatched dogwhelks (*N. lapillus*) were first starved for 5–10 d, to standardize hunger levels, and then put individually in 10 plastic cages with a range of sizes of one potential prey species, either slippershell snails (*C. fornicata*), mussels (*M. edulis*), or barnacles (*S. balanoides*). The latter 2 species were used as positive controls, since *N. lapillus* preys readily on both mussels and barnacles (Hughes and Dunkin, 1984; Palmer, 1984; Petraitis, 1990; Burrows and Hughes, 1991). Plastic cages used in all experiments were lidded plastic boxes (5×5×4.4 cm) with 2 opposing sides removed and covered with Nitex mesh (0.5 mm mesh size) to allow for water circulation. Lids were closed and the cages were submerged in an aquarium of seawater (again, filtered to 1 μm), which received constant aeration. Prey species were fed by adding the phytoplankton *I. galbana*, clone T-ISO, to reach a concentration of approximately 2×10^5 cells ml^{-1}. Additional phytoplankton was added daily as needed, and water was changed several times weekly.

Prey consumption was monitored once or twice weekly for up to 3 months or until all dogwhelks had died. Evidence of consumption included shells or tests with drill holes, or, for barnacles, tests that were entirely clean of tissue. In nearly all cases, when a barnacle test was clean of tissue we found a drill hole in one of the valves. This was not the case when there was tissue remaining in the test of a dead barnacle, and so these barnacles were conservatively assumed to have died from other causes. New prey were replaced with individuals similar in size to the dead ones (except for *S. balanoides*, which were attached to rocks, a natural substrate, and therefore were not replaced).

Since newly hatched dogwhelks did not feed on barnacles or on *C. fornicata* (see Section 3), these experiments were later repeated using larger juvenile dogwhelks. Juvenile dogwhelks that hatched from egg capsules in the lab were kept in plastic cages with mussels for 2–3 months until they had grown to at least 5 mm shell length. The dogwhelks were then randomly assigned to cages containing small juveniles of either *C. fornicata* or *S. balanoides*.

To check whether dogwhelks (*N. lapillus*) that did not drill any of the prey offered in some treatments were nevertheless capable of feeding and growing under our laboratory conditions, we determined dogwhelk growth rates for individuals offered an accepted diet: the blue mussel *M. edulis*. The shell length for each dogwhelk (the distance from the shell apex to the tip of the siphonal canal) was measured at 8–50× magnification at the beginning of the experiment, using a dissecting scope equipped with an ocular micrometer, and re-measured periodically until either the dogwhelk had died or the experiment was ended. The mean sizes of predators and prey used in each experiment are shown in Table 1.

Table 1
Dimensions of predators and prey in experiments with the dogwhelk, *Nucella lapillus*, offered various potential prey. All sizes are mean ± 1 SD for all replicates, and were measured at the beginning of each experiment using a dissecting scope equipped with an ocular micrometer (8–50×). Shell length (SL) of dogwhelks was the greatest distance from the apex to the tip of the siphonal canal. Lengths for prey species were all the greatest distances across the shell (measured from the umbo or protoconch) or the greatest basal diameter for barnacles.

Starting SL of *Nucella lapillus* (mm) and # of replicates	Prey	Prey size (mm) and # of prey/replicate	Growth rate (mm SL d^{-1})
1.1 ± 0.1, $n=7$	*Crepidula fornicata*	5.3 ± 3.0, $n=6$	0
9.0 ± 3.1, $n=7$	*Crepidula fornicata*	8.6 ± 2.7, $n=3$–6	0
1.4 ± 0.3, $n=10$	*Mytilus edulis*	5.0 ± 2.3, $n=9$	0.17 ± 0.01
1.2 ± 0.1, $n=10$	*Semibalanus balanoides*	7.4 ± 1.9, $n=3$–43	0
5.1 ± 2.6, $n=10$	*Semibalanus balanoides*	4.8 ± 1.8, $n=8$–37	0.13 ± 0.10

2.3. U. cinerea as a potential predator of C. fornicata

These experiments were similar to those conducted with *N. lapillus*; however, since oyster drills are known to prey on adults of *C. fornicata* (Pratt, 1974a) we also tested whether they prey selectively on *C. fornicata*. In each experiment, recently hatched oyster drills were given a choice of feeding on either recently metamorphosed slippershell snails or on small field-collected mussels (*M. edulis*) of similar shell length, or were offered a choice of recently metamorphosed slippershell snails or barnacles (*S. balanoides*) of similar size. Prey species – both are suspension-feeders – were fed daily with a mixture of phytoplankton (about 50% *I. galbana*, clone T-ISO and 50% *Dunaliella tertiolecta*, clone DUN). Finally, since oyster drills fed on all prey species offered, experiments were terminated after only 2 weeks.

Every 3–4 days for 2 weeks the prey animals in all containers were inspected for evidence of predation, indicated by empty shells and conspicuous counter-sunk holes drilled into the shells (Harding et al., 2007). The drilled shell and the responsible oyster drill were measured at 12–32× using a dissecting microscope equipped with an ocular micrometer. During the experiment, individuals of *C. fornicata* grew to lengths of up to 7.5 mm and the mussels grew to lengths of up to 5.2 mm.

A similar experiment was conducted using slippershell snails and barnacles. The barnacles were collected on small stones at Nahant, MA. Excess barnacles were removed from the stones before use, so that only 3 small barnacles were living on each stone. The barnacle tests were approximately 3.5 mm in diameter at the start of the experiment. For each of 8 replicates we included one recently hatched oyster drill as predator and 3 barnacles and 3 slippershell snails as potential prey.

One experiment was conducted in which newly hatched oyster drills were confined only with recently metamorphosed individuals of *C. fornicata* (1 oyster drill and 6 slippershell snails per container, with 8 replicates). At the start of the study, the oyster drills had an average shell length of 1.4 mm (SD = 0.5 mm, $n = 8$) and the slippershell snails had an average shell length of 2.7 mm (SD = 0.5 mm). Observations were made for 7 days.

2.4. Field evidence for U. cinerea predation on C. fornicata

A haphazard sample of 230 empty shells of *C. fornicata* was collected intertidally on a spring low tide at Bissell Cove, Rhode Island, in October 2003, a site with large populations of both *C. fornicata* and *U. cinerea*, and with very large numbers of empty *C. fornicata* shells. The empty shells were between 13.3 and 39.8 mm long. We have never observed any individuals of *N. lapillus* at this site. Another 683 empty but intact shells of *C. fornicata* were collected from the same site the following year (October 2004). The collected shells were again mostly between about 13 and 40 mm in length, with one additional shell at only 6.5 mm in shell length. The shells were individually inspected for drill holes, and all drilled shells were measured.

2.5. H. sanguineus as a potential predator of C. fornicata

2.5.1. Animal collection and care

Shore crabs (*H. sanguineus*) and adults of *C. fornicata* were collected from Nahant, MA. Shore crabs were maintained in the laboratory on a diet of brine-shrimp pellets and imitation crab meat, while snails were fed the naked flagellates *I. galbana* (clone T-ISO) and *D. tertiolecta* (clone DUN) as described above. Juveniles of *C. fornicata* were obtained by rearing larvae and inducing metamorphosis as described previously. Juveniles were used in experiments 1 day after they had been induced to metamorphose. In order to rule out family-specific effects, we conducted each experiment using the combined hatches from two different females.

Because female and male shore crabs differ in the shape of their claws and in their predatory behavior (Bourdeau and O'Connor, 2003), we tested male and female shore crabs separately. Although the crabs were collected haphazardly, we found only 5 females, and so the female-crab treatment consisted of only 5 replicates. To determine how predator size would affect predation intensity, we separated male crabs into two size categories: “small” males with carapace widths between 10.5–13.0 mm ($n = 11$) and “large” males with carapace widths between 14.5–18.0 mm ($n = 9$). The carapace widths of females ranged from 13.8 mm to 17.3 mm (mean ± SD = 16.02 mm ± 1.36, $n = 5$).

2.5.2. Predation experiments

In order to determine whether *C. fornicata* juveniles are subject to predation by shore crabs, and whether they achieve an escape in size from predation by growth, we measured the shore crabs' levels of predation on the snails at 1 d and again at 10 d after the *C. fornicata* larvae had metamorphosed. Within one experiment, the same shore crabs were used for tests at both time points.

Shore crabs were starved for 2 d before being presented with juvenile snails. Each shore crab was placed in a 7.6 cm-diameter glass dish of Instant Ocean with 5 juvenile snails and left in the dish for 19 h. We recorded the number of snails still present at the end of that time period; missing juveniles were presumed to have been eaten by the crabs. This was a safe assumption, given that juveniles in dishes with dead crabs or empty shells were all still visible after 19 h. Remaining juveniles were removed from dishes at the end of the experiment and were not reused. Results were analyzed using repeated-measures ANOVAs (GraphPad Prism 4 software). For statistical analysis, the predation results for large and small male crabs and for female crabs were combined if the number of snails eaten did not differ significantly among the categories at any time point.

2.6. P. longicarpus as a potential predator of C. fornicata, C. convexa, and C. plana

2.6.1. Animal collection and care

Hermit crabs preyed heavily on juveniles of *C. fornicata*, and so additional feeding studies were conducted using this predator, to determine the influence of shell morphology on vulnerability to predation. Hermit crabs (*P. longicarpus*) and adult snails of three co-occurring species (*C. fornicata, C. convexa,* and *C. plana*) were collected intertidally from Nahant, MA. All animals were kept in the lab in aerated Instant Ocean. Hermit crabs were maintained on a diet of brine-shrimp pellets, while snails were fed phytoplankton as described above. Juveniles of *C. fornicata* and *C. plana* used in experiments were reared in the laboratory from larvae as described previously. The juveniles were used 1 day after they metamorphosed; for *C. convexa,* juveniles were used 1 day after they emerged from under the mother's shell.

For all three snail species, we conducted each experiment using the combined hatches from two different females, in order to eliminate family-specific effects.

To determine whether the relative size of the predator would affect its level of predation, hermit crabs were separated into two size categories for the experiments: “small” crabs in shells with apertures between 8.5–10.5 mm in diameter, and “large” crabs in shells with apertures between 14–16 mm.

2.6.2. Predation experiments

In order to determine whether *Crepidula* juveniles are subject to predation by hermit crabs, and whether they achieve an escape in size from predation during the first week or two of juvenile life, we conducted experiments using approximately the same methods as those used for *H. sanguineus.* We measured the hermit crabs' levels of predation on the snails at three time points: 1 day, 4–5 days, and 9–15 days after juveniles had first metamorphosed (or hatched as

juveniles, in the case of *C. convexa*). Within each experiment, the same hermit crabs were used for the duration of the study.

For statistical analysis, predation results for large and small hermit crabs were combined if the number of snails eaten did not differ significantly ($p > 0.10$) for the categories at any time point. Large and small hermit crabs did not differ in their degree of predation except when preying on *C. convexa* juveniles (Section 3).

2.6.3. Juvenile shell calcification

If larger juvenile snails were preyed on by hermit crabs less often than smaller juvenile snails, the decreased predation intensity might be due to increasing shell thickness as the snail prey grew. To determine the extent to which the *Crepidula* juveniles' shells were calcifying over time, we obtained ash-weight data using juveniles within the size ranges of our experimental animals. Juvenile shell lengths were determined and the juveniles were then killed, dried for 24 h at 55 °C in preweighed foil pans, and weighed. They were then maintained at 520–550 °C for 12 h to oxidize organic content; the resulting ash weight was then determined, and ash-free dry weight was calculated by difference. The relationship between shell thickness (shell weight divided by length) to shell length was analyzed by linear regression (GraphPad Prism 4 software). Data for *C. plana* were collected during the course of these experiments, in 2002; data for *C. fornicata* and *C. convexa* were collected during previous studies (Pechenik and Eyster, 1989; Li and Pechenik, 2007).

3. Results

3.1. N. lapillus as a potential predator of C. fornicata

Remarkably, juvenile dogwhelks (*N. lapillus*), whether newly hatched or older, ate none of the *C. fornicata* juveniles offered in our study (Table 1); instead, all dogwhelks offered only *C. fornicata* as prey died within 1–2 months of the start of the experiment, without ever eating. While this was also true for newly hatched dogwhelks offered only barnacles (only 1 of the 10 dogwhelks ate any barnacles in nearly 2 months), older juvenile dogwhelks readily fed on barnacles, and even newly hatched dogwhelks fed on mussels. There was variation in the number of mussels consumed per predator, but predator growth rates were consistent among individuals (Table 1); over a period of about 2.5 months on a diet of mussels, young dogwhelks increased in shell length from about 1.5 mm to about 15 mm (data not shown). The size range of consumed prey was similar for mussels and barnacles, and this range spanned the shell lengths (SL) of all but 2 of the slippershell snails that had also been offered as food (2.2–11.4 mm SL offered to newly hatched dogwhelks, and 5.3–15.5 mm SL offered to older dogwhelks). There were drill holes in the shells of all consumed mussels, and in most of the shells of consumed barnacles (mostly in the valves, although a few barnacles had been drilled through their lateral plates). In contrast, no *C. fornicata* shell bore any signs of attempted drilling. The mean growth rate of dogwhelks feeding on barnacles was similar to the mean growth rate of those feeding on mussels, but the variation in growth rates was 10 times higher (Table 1).

3.2. U. cinerea as a potential predator of C. fornicata

Over the two-week observation period, recently hatched oyster drills ate 3 times as many mussels as slippershell snails (Table 2). The sizes of consumed prey were similar for the 2 prey species (Table 2).

When given the choice of slippershell snails or barnacles as prey, recently hatched oyster drills ate only barnacles; no slippershell snails were drilled, and all were alive at the end of the 10 day observation period. Moreover, whereas oyster drills were often seen on the barnacles, they were never observed on any *C. fornicata* shell.

Only one of the dead barnacles was drilled during the 10-day observation period; the others either died and were subsequently eaten, or were killed by the predator inserting its proboscis between the shell plates; oyster drills grew to lengths of up to 2.7 mm during this study.

Table 2
Predation by oyster drills, *Urosalpinx cinerea*, when given a choice of feeding on slippershell snails (*Crepidula fornicata*) or mussels (*Mytilus edulis*). Each of 12 containers held one recently hatched oyster drill, 3 young slippershell snails, and 3 young mussels of similar size.

Prey	Total no. eaten	Mean prey size (mm)	SD	Range in prey size (mm)
Crepidula	5	2.8	0.8	2.0–4.1
Mussels	15	3.2	0.6	1.8–4.0

When oyster drills were confined only with recently metamorphosed *C. fornicata* juveniles, 3 of the 8 oyster drills together drilled and consumed 6 slippershell snails; one of the empty *C. fornicata* shells exhibited 2 drill holes. None of the other 5 oyster drills killed any of the slippershell snails offered to them; however, in one of the cages, the shell of one slippershell snail bore 3 drill holes, although the snail itself was not killed or eaten.

3.3. Field evidence of predation on C. fornicata

Of the 230 empty shells of *C. fornicata* collected from Bissel Cove, RI inspected in 2003, 8 (3.5%) exhibited drill holes made by the oyster drill *U. cinerea*. All the other shells collected at this site were intact. Of the 8 shells that had been drilled, one was the largest shell in the collection (39.8 mm) while the other was the smallest (13.3 mm). For the second sample of empty shells, collected from the same site in Fall 2004, 19 out of 683 shells (2.8%) examined had been drilled. Drilled *C. fornicata* shells ranged between 18.6 and 33.5 mm in shell length (Mean = 28.2 mm, SD = 5.1, $n = 19$).

3.4. H. sanguineus as a potential predator of C. fornicata

Both male and female shore crabs preyed heavily on *C. fornicata* juveniles, and these levels of predation did not differ significantly among large male, small male, or female predators (two-way repeated-measures ANOVA, $F_{2,19} = 0.4941$, $p = 0.6177$). While the crabs ate an average of 4 out of 5 *C. fornicata* juveniles 1 day after the juveniles had metamorphosed, levels of predation on the juvenile snails increased significantly over time as the snails grew (two-way repeated-measures ANOVA, $F_{1,19} = 5.401$, $p = 0.0314$; Fig. 1).

3.5. P. longicarpus as a potential predator of C. fornicata, C. convexa, and C. plana

Hermit crabs ate on average at least 4 out of the 5 *C. fornicata* juveniles presented to them (Fig. 2A). Predation levels did not decrease significantly as the juvenile snails grew and thickened their shells (repeated-measures ANOVA, $F_{2,13} = 1.216$, $p = 0.3127$); crabs ate approximately the same number of older, larger juveniles as younger, smaller ones (Fig. 2A).

Hermit-crab predation on *C. plana* juveniles was more moderate, with crabs eating, on average, only 2 or 3 of the 5 small juveniles presented to them, and eating even fewer when the snail prey were larger (Fig. 2B). This decrease in predation by hermit crabs over time (Fig. 2B) was statistically significant (repeated-measures ANOVA, $F_{2,19} = 8.26$, $p = 0.011$).

Finally, there was no significant difference in the number of *C. convexa* juveniles preyed on by large hermit crabs over time (repeated-measures ANOVA, $F_{2,6} = 2.211$, $p = 0.152$), and predation on even the larger juveniles never went below 3–4 out of 5 snails being eaten per hermit crab (Fig. 2C), even as shells thickened considerably as the snails grew (Fig. 3C). Small hermit crabs showed a tendency to eat more

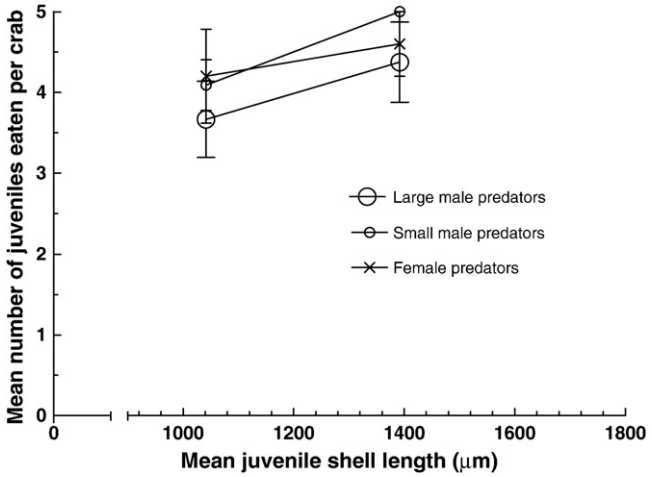

Fig. 1. Predation by shore crabs (*Hemigrapsus sanguineus*) on *C. fornicata* juveniles at two time points, 1 day and 10 days after metamorphosis. The corresponding mean sizes of the juveniles on those days are shown on the *x*-axis. Male shore crabs were classified as either large ($n=9$) or small ($n=11$); females ($n=5$) were kept as one group. Crabs were placed in glass dishes with 5 juvenile snails, and their levels of predation were recorded after 19 h.

C. convexa juveniles at later time points (Fig. 2C), but this trend was not significant (repeated-measures ANOVA, $F_{2,9}=2.88$, $p=0.086$).

3.6. Changing shell thickness over time

For all 3 *Crepidula* species, juvenile shell thickness increased significantly with increasing shell length (*C. fornicata*, $r^2=0.889$, linear regression $F_{1,65}=521.1$, $p<0.0001$; *C. plana*, $r^2=0.72$, regression $F_{1,42}=106.9$, $p<0.0001$; *C. convexa*, $r^2=0.58$, regression $F_{1,47}=65.2$, $p<0.0001$ [Fig. 3]). For shells of a given length (e.g., 2 mm), those of *C. convexa* were considerably thicker than those of the other 2 species (Fig. 3).

4. Discussion

The levels of predation on juvenile *C. fornicata* varied greatly in this study, from no predation at all by the dogwhelk *N. lapillus*, even when those predators were offered nothing else to eat for several months, to near-complete predation by hermit crabs (*P. longicarpus*) and shore crabs (*H. sanguineus*). Juveniles of *C. fornicata* are clearly not equally vulnerable to all predators, but our study confirms that they can and will be preyed upon by at least some drilling snails (*U. cinerea*) and by at least some crustaceans (*P. longicarpus* and *H. sanguineus*). Shore crabs ate almost all *C. fornicata* juveniles presented to them even 10 days after the snails metamorphosed, when the snails had shells as long as 1.5 mm (Fig. 1). Although *H. sanguineus* is also known to eat some other molluscs (the mussel *M. edulis*, the clam *Mercenaria mercenaria*, and to a much lesser extent, the snail *Littorina littorea*—Bourdeau and O'Connor, 2003; Brousseau and Baglivo, 2005), this is the first indication that it may feed extensively on juvenile *C. fornicata* as well.

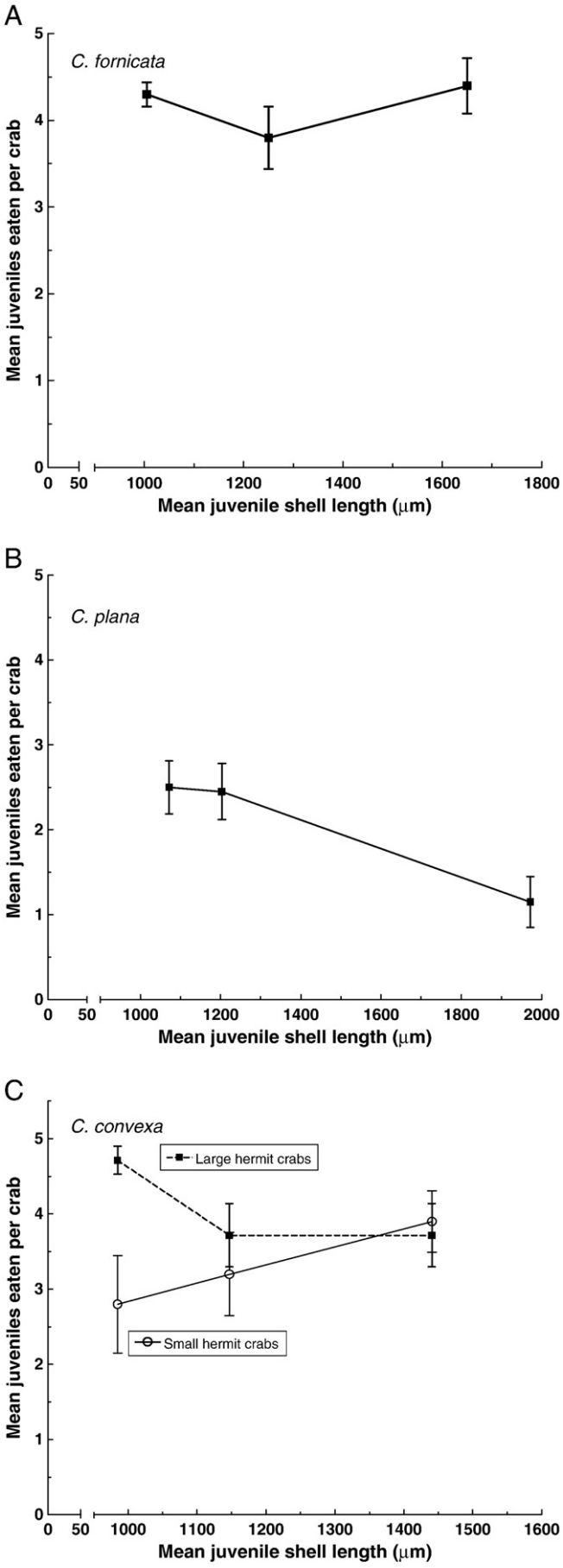

Fig. 2. A) Predation by hermit crabs (*P. longicarpus*) on *C. fornicata* juveniles at 1 day, 5 days, and 15 days after metamorphosis. The corresponding mean sizes of the juveniles on those days are shown on the *x*-axis. Each hermit crab ($n=20$) was placed in a dish with 5 juvenile snails for 17–19 h. B) predation by hermit crabs on *C. plana* juveniles at 1 day, 4 days, and 11 days after metamorphosis. The corresponding mean sizes of the juveniles on those days are shown on the *x*-axis. Each hermit crab ($n=20$) was placed in a dish with 5 juvenile snails for 17–19 h. C) Predation by hermit crabs on *C. convexa* juveniles at 1 day, 4 days, and 9 days after hatching. The corresponding mean sizes of the juveniles on those days are shown on the *x*-axis. Each hermit crab (10 large, 10 small) was placed in a dish with 5 juvenile snails for 17–19 h.

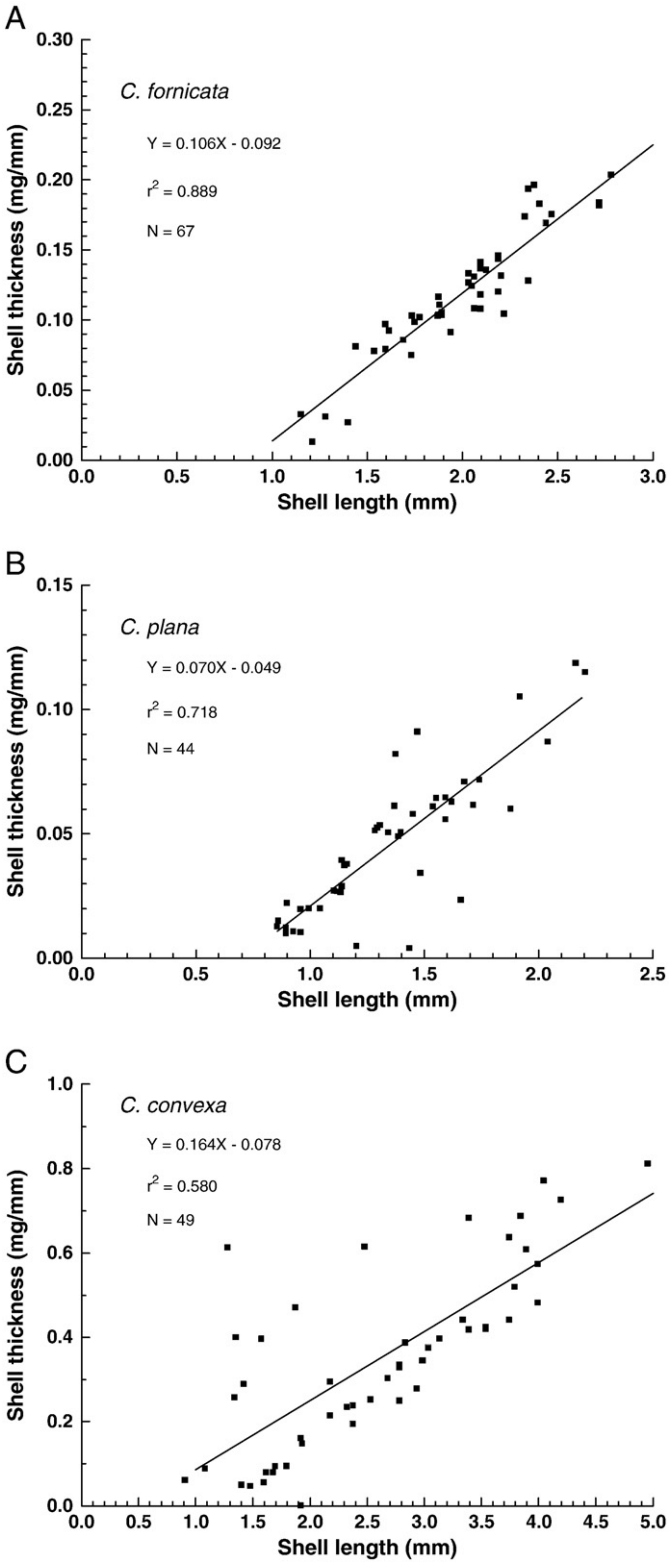

Fig. 3. Changes in juvenile shell thickness (weight divided by length) over time as a function of shell length for *C. fornicata* (A), *C. plana* (B), and *C. convexa* (C).

Hermit crabs also ate most of the *C. fornicata* juveniles presented to them, even 15 days after metamorphosis when the *C. fornicata* shells exceeded 1.5 mm in length; the fact that these snails remained vulnerable to hermit-crab predators even after 2 weeks of growth and increased shell thickness (Fig. 3A) suggests that *C. fornicata* does not achieve a very quick escape in size from these common and potentially rapacious predators. *C. fornicata* juveniles might even become more vulnerable to shore crabs as they grow, as predation levels on *C.fornicata* juveniles were significantly higher 10 days after the snails metamorphosed than when the snails were much younger. Given that observed mortalities of other juvenile gastropods have ranged from 24–92% within their first month in the benthos (reviewed in Gosselin and Qian, 1997), the willingness of hermit crabs, shore crabs, and oyster drills to eat *C. fornicata* juveniles that were at least 1.5–2 weeks old (crabs) or between 2–4 mm long (oyster drills) speaks to the impact such predators could have on the growth of local *C. fornicata* populations.

Hoagland (1974) suggested that dogwhelks (*N. lapillus*) fed on *C. fornicata* in Woods Hole. In our study, however, young dogwhelks did not eat any *C. fornicata* juveniles even when given no other choice of prey; indeed, the dogwhelks used in our study never even attempted to eat those prey, and eventually starved to death in their presence. The rapid and substantial growth of dogwhelk predators on a diet of blue mussels during this study indicates that the predators were able to locate and drill prey in the laboratory; thus their failure to eat *Crepidula* is not likely an artifact of adverse laboratory conditions.

The lack of interest by *N. lapillus* in juveniles of *C. fornicata* seen in our study is also not likely due to a mechanical defense on the part of the juveniles, since, firstly, the other predatory gastropod, the oyster drill *U. cinerea*, had no difficulty in boring holes through the shells of juvenile *C. fornicata*, and, secondly, there was no evidence that dogwhelks had even attempted to drill into the *Crepidula* shells. Either the dogwhelks did not recognize juvenile *C. fornicata* as prey, or the *C. fornicata* juveniles discouraged predation by chemical means; dogwhelks and other muricids clearly use chemical cues in locating their prey (Carroll and Wethey, 1990; Wood, 1968; Brown and Rittschof, 1984; Vadas et al., 1994). Any failure of recognition is not likely due to lack of sufficient length of contact between predator and potential prey in the native habitat: dogwhelks have been in New England for thousands of years (Collins et al., 1996; Wares and Cunningham, 2001). We note also that *Hemigrapsus* was a voracious predator of juvenile *Crepidula* even though *H. sanguineus* has been in MA waters for less than 20 years (McDermott, 1998; Bourdeau and O'Connor, 2003). The response of older dogwhelks to juvenile *C. fornicata* merits further study, as does their possible willingness to eat older and larger slippershell snails.

Although oyster drills (*U. cinerea*) ate no *C. fornicata* juveniles when given the option of eating barnacles in the laboratory, they did prey on *C. fornicata* juveniles to a degree when those juveniles were offered either with mussels or alone. The rarity (only about 3% of the 913 empty shells examined) of drill holes that we observed in adult *C. fornicata* shells collected from Bissel Cove, RI suggests that our laboratory experiments reflect naturally low levels of oyster-drill predation on *C. fornicata* in the field, although predation in the field might be somewhat higher than that inferred for adults: in no-choice situations in the laboratory we observed 12.5% mortality of *C. fornicata* juveniles (6 out of 48 snails were eaten), and in mussel-*C. fornicata* choice experiments we observed 13.9% mortality of *C. fornicata* juveniles (5 out of 36 snails were eaten). Hoagland (1974) reported that only about 1% of empty *C. fornicata* shells collected subtidally from Vineyard Haven, MA had been drilled, but that drill holes were present in about 5% of *C. fornicata* shells collected from a beach in Woods Hole. Oyster drills locate their prey by chemoreception of prey odors (Wood, 1968; Pratt, 1974a; Brown and Rittschof, 1984), suggesting that *C. fornicata* may produce a less attractive or more dilute odor than, for example, oysters. Adults of *C. fornicata* also exhibit behavioral defenses (biting with the radula and pivoting) against adult *U. cinerea* (Pratt, 1974b); it remains to be determined whether such defenses are displayed (or are effective) by juvenile *C. fornicata* in response to attacks by juvenile oyster drills. Oyster drills are commonly thought to specialize on barnacle and mussels as prey (Carroll and Wethey, 1990; Petraitis, 1990).

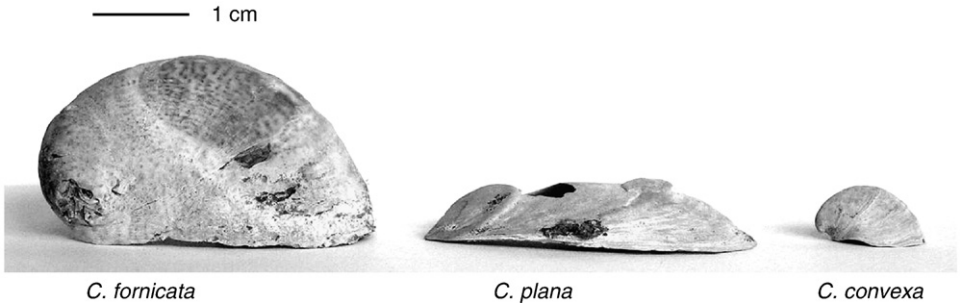

Fig. 4. The shell shapes of all 3 *Crepidula* species included in this study: *C. fornicata, C. plana*, and *C. convexa*.

Our results suggest that hermit crabs are major predators of juvenile *C. fornicata* in New England. In contrast, hermit crabs of 3 tested pagurid species failed to eat any juvenile abalones (*Haliotis kamtschatkana*) in laboratory choice experiments reported by Konishi and Uki (1993) and by Griffiths and Gosselin (2008). This intriguing disparity should be investigated. Of the 3 sympatric *Crepidula* species included in our study, juveniles of *C. fornicata* appeared to be the most vulnerable to hermit-crab predation, experiencing higher levels of predation than juveniles of either of the 2 other species at comparable shell sizes and showing no escape in size within the time period of the study (Fig. 2A). *C. plana* juveniles were the least vulnerable in our study, experiencing on average the lowest levels of predation (about 45% were eaten) even for newly metamorphosed individuals (Fig. 2B) and achieving a substantial degree of escape in size: by 11 days after metamorphosis, when their average shell length was almost 2 mm, predation levels had been reduced to less than half what they were earlier in the study (Fig. 2B). *C. convexa* juveniles experienced intermediate levels of predation and were the only species for which hermit-crab size may have influenced predation intensity (Fig. 2C).

The difference in degrees of predation by hermit crabs upon the 3 *Crepidula* species included in our study may reflect the hermit crabs' method of predation and the differences in shell morphology among the 3 *Crepidula* species. During our experiments, we observed hermit crabs prying intact juvenile snails from the substrate and then consuming the juveniles, shell and all. The hermit crabs were never observed smashing the juveniles' shells, and in no dish were shell fragments ever found. The efficacy, then, of a feeding strategy that involves pulling a snail from its substrate, rather than smashing through its shell, would necessarily be affected by shell morphology. *C. plana* snails are, as the name implies, extremely flat (Coe, 1938; Fig. 4). With little to grip, the shells of *C. plana* snails were probably especially difficult for hermit crabs to remove, especially as the juveniles grew and adhered more tightly to the substrate. *C. fornicata* and *C. convexa*, however, have more rounded shells (Fig. 4), which should make them easier to grasp and pry loose from a substrate.

Our study of predation on *C. fornicata* juveniles by 4 common native predators suggests that some molluscan and especially crustacean predators could severely limit recruitment of slippershell snails into adult populations in the field. Although oyster drills preferred mussels when given a choice of prey in the laboratory, they nevertheless ate almost 14% of the *C. fornicata* juveniles presented to them. Hermit and shore crabs ate an average of 60–100% of the juveniles presented to them. The success of *C. fornicata* as an invasive species in France and elsewhere may be due in large part to a release from predators such as hermit and shore crabs (and to a lesser extent from some drilling gastropods), either because of smaller numbers of such predators in the new environment or because those predators prefer native prey over the invasive species or do not yet recognize the invaders as potential prey. More work is needed both at home and abroad to identify the types of predators and the degree of predation pressure these snails face in the field, particularly as recently metamorphosed juveniles.

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