Size-specific predation by dominant consumers maintains a 'trophic cul-de-sac′

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ABSTRACT: Manipulations of fully grown (>60.0 mm) detritivorous Sydney mud whelks *Pyrazus ebeninus* Brugiere 1972 suggest that the species serves as a 'trophic cul-de-sac', limiting flow of carbon from producers to top consumers. However, although large *P. ebeninus* individuals experience negligible predation, smaller individuals that do not cause the same depletion of primary and secondary producers may suffer predatory losses. To assess the role that predation on the small whelks might play in weakening the trophic cul-de-sac provided by larger conspecifics, we investigated size- and habitat-specific patterns of predation on *P. ebeninus* through a series of field and laboratory experiments. Field tethering of 3 size classes of snail indicated that irrespective of seasonal differences in predation intensity, small (30.1 to 40.0 mm shell height, SH) individuals experienced significantly greater predatory mortality (25% over 7 wk) than medium (50.1 to 60.0 mm SH: 7.5%) or large (70.1 to 80.0 mm SH: 2%) conspecifics. Predatory mortality was largely attributable to naticid predators, although several tethered snails were crushed, perhaps by elasmobranchs, toadfish or crabs. For some size classes there were differences in predatory mortality between low shore mudflats and higher shore mangrove forests, but the direction of these differences varied between autumn and spring, and the differences disappeared altogether when densities of predators were held constant, indicating that they were not driven by habitat per se. In laboratory experiments, the relative contributions of small, medium and large *P. ebeninus* individuals to the total prey consumed by the naticid gastropod *Conuber sordidus* Swainson 1821 were similar between choice and no-choice experiments, and even in the absence of small prey items, large *P. ebeninus* snails were not consumed. Thus, even when there is depletion of small size classes of *P. ebeninus*, it is unlikely that common benthic predators would consume sufficient numbers of large snails to prevent deleterious effects of this species on primary and secondary production. To the contrary, predatory mortality of small *P. ebeninus* individuals may ensure that its populations continue to be dominated by the large, damage-causing size classes.

KEY WORDS: Detritus-based food web · Naticid · Predation · *Pyrazus ebeninus* · Trophic cul-de-sac

INTRODUCTION

As mediators of carbon flow from decaying organic matter to higher trophic levels, detritivorous invertebrates are key determinants of the diversity, structure and dynamics of communities (Moore et al. 2004). Detritivorous invertebrates directly consume detritus or microorganisms (e.g. diatoms) stimulated by detrital break-down (Findlay & Tenore 1982, Rublee 1982,

Lopez & Levinton 1987). The detritivorous invertebrates are eaten by bottom dwelling fishes and these, in turn, serve as prey to piscivorous fish (Edgar & Shaw 1995, Melville & Connolly 2003). Depending on the productivity of systems, decomposers and detritivores may consume 100 to 300% as much carbon as herbivores (Cebrián & Latrigue 2004).

Although aquatic consumers can be very efficient at turning over ingested carbon and transferring it to

higher trophic levels (Cebrián 2004), increasing evidence suggests that this is not always the case (Bishop et al. 2007a). Some large detritivorous invertebrates appear to short-circuit trophic transfer by decreasing the abundance of other softer-bodied or smaller invertebrates that are important prey sources for consumers, such as birds and fish, while themselves suffering negligible predation. Recent experiments suggest that the Sydney mud whelk *Pyrazus ebeninus* Brugiere 1972 may be one such 'trophic cul-de-sac' (Bishop et al. 2007a). Increasing the density of large (76 ± 0.6 mm [mean ± SE], n = 75) *P. ebeninus* individuals from 4 to 44 m^{-2} halved the abundance and diversity of macroinvertebrates. Over 2 mo, no predatory mortality of thick-shelled *P. ebeninus* was observed and high densities of this species decreased the effects of vertebrate predators on macroinvertebrate abundances, suggesting compromised trophic transfer (Bishop et al. 2007a). These results strongly suggest that the energy consumed by the snail may only become biologically available once the snail dies, and even then, only to scavengers and detritivores that occupy lower trophic levels of the food web.

Despite the strong evidence that large *Pyrazus ebeninus* whelks limit flow of energy up the food web to commercially important species, the influence of smaller individuals on the strength of the cul-de-sac has not been considered. Many benthic predators have size-selective feeding relating to (1) vulnerability and catchability of the prey items, (2) their energetic value and (3) risk to the predator of injury during foraging (reviewed by Hughes 1980). Thus, in contrast to large *P. ebeninus* individuals, which appear to experience negligible predation, smaller snails may be susceptible to benthic predators such as smooth toadfish *Tetractenos glaber* and natcid gastropods of the genus *Conuber*, which are known to be prey size-selective (Bayliss 1986, Anderson & Connell 1999). Although unlikely to fully compensate for depletion of other prey resources by fully grown *P. ebeninus*, predation on smaller specimens could weaken the trophic cul-de-sac by allowing some carbon flow up the food web, reducing the number of individuals reaching the cul-de-sac size class and limiting the total population size attained by *P. ebeninus.* If, however, predators are capable of eating small and large *P. ebeninus* but choose smaller over larger individuals when both are available, predation on smaller snails may, to the contrary, be the reason the trophic cul-de-sac exists.

Understanding the role that size-selective predation plays in modifying the strength of trophic cul-de-sacs is of critical importance for the management of marine and estuarine systems given the likelihood that trophic dead-ends are common components of benthic food webs and the large effects these may have on the responses of systems to perturbations (Blomqvist 1996, Bishop et al. 2007a). Like *Pyrazus ebeninus,* several other gastropod species (e.g. *Illyanassa obsoleta, Strombus gigas*) appear to exhibit characteristics of trophic cul-de-sacs in that they lack predators (Ray et al. 1994, Tucker et al. 1997), with concomitant negative effects on secondary producers (Kelaher & Levinton 2003, Kelaher et al. 2003). In the present study, we examine the role of size-selective predation in modifying the strength of the trophic cul-de-sac provided by *P. ebeninus.* We hypothesized that greater numbers of small (30.1 to 40.0 mm shell height, SH) than medium (50.1 to 60.0 mm SH) or large (70.1 to 80.0 mm SH) *P. ebeninus* individuals are consumed by benthic predators and that this size-selective predation will ensure that the mean size of *P. ebeninus* remains within the range known to produce the trophic cul-de-sac.

To better understand the mechanism underlying any size-selective predation, and hence how the cul-de-sac may be influenced by changes in the availability of prey size classes, we singled out a key predator (the naticid gastropod *Conuber sordidus* Swainson 1821) for experiments examining whether size-selectivity is dependent upon the availability of the most vulnerable size classes. Naticid gastropods are well known to display stereotypic predation whereby prey are detected, evaluated, seized, covered and immobilized with copious pedal mucus, wrapped in the dilated foot, and then carried deep into the sediment for commencement of boring (e.g. Hughes 1985). We hypothesized that even in the absence of small *Pyrazus ebeninus* individuals, the predator will consume negligible numbers of this prey because selectivity is driven by prey vulnerability and stereotypy of predatory behaviour, rather than preference of the predator for particular size classes of prey. Finally, to understand how the strength of the trophic cul-de-sac might vary spatially, we determined how habitat characteristics influence predation rates of the dominant consumer on the most vulnerable size class of *P. ebeninus.* Because naticid gastropods consume prey items underground, we hypothesized that dense mats of vegetation (seagrass or pneumatophores) will impede predator burial, decreasing the foraging efficiency of *Conuber sordidus* on *P. ebeninus*, thereby reducing any leak in the cul-de-dac.

MATERIALS AND METHODS

Study sites. Field experiments were done in Quibray Bay, on the south side of Botany Bay (33° 59′ S, 151° 12′ E), New South Wales, Australia. This location supports sizeable populations of *Pyrazus ebeninus* throughout the intertidal zone, with adults (>60 mm SH) most abundant on the Botany Bay's mudflats and

juveniles (<60 mm SH) predominantly (though not exclusively) higher on the shore in the mangroves (Bishop et al. 2007a). Experiments were conducted at 2 sites in the mid-shore mangrove zone (Mean Low Water, MLW + 0.8 m) and 2 on the low shore mudflats (MLW + 0.5 m). The mid-shore sites had a pneumatophore density of $550 \pm 60 \text{ m}^{-2}$ (mean ± SE, n = 10). The low shore mudflats were vegetated with stunted paddleweed *Halophila ovalis*, and stunted eelgrass *Zostera capricornii*. All study sites contained natural populations of *P. ebeninus*, measured 5×5 m and were separated by hundreds of meters from one another.

Laboratory experiments were conducted in $420 \times 245 \times 280$ mm aquaria containing a 70 mm base of muddy sand and a water depth of 200 mm. Snails were permanently submerged in the aquaria because previous studies suggest that naticids are unable to move through dry or even moist sand; they feed by searching waterlogged sediments for prey (Kitching et al. 1987). Aquaria received aerated seawater from a filter at a rate of 200 l h^{-1} and were exposed to a 12:12 h photoperiod generated by UV lights held 265 mm above the tanks. To minimize variability in feeding rates, water temperature (22°C) and salinity (35 ppt) were held constant across replicates. The sediments used in the aquaria were sieved through a 6.7 mm screen immediately after collection from Quibray Bay. Sieving removed large infauna (that may otherwise have served as alternative prey for *Conuber sordida*) while retaining the detritus to support *Pyrazus ebeninus*. Each tank was covered with 10 mm polyvinyl chloride (PVC) mesh to prevent the snails from escaping.

Field assessments of size-specific predatory mortality. We assessed size-specific rates of *Pyrazus ebeninus* mortality attributable to predation in the autumn and spring of 2006. We selected 3 size classes of *P. ebeninus* in our assessments, hereafter referred to as small (30.1 to 40.0 mm SH), medium (50.1 to 60.0 mm SH) and large (70.1 to 80.0 mm SH). For each site and season, 20 snails of each size class were deployed in a 5×5 m grid in haphazard order of sizes. To ensure traceability of individuals, which may be dragged underground by certain predators, and to standardize deployment across sites and time periods, snails were attached to 400 mm long tethers. Tethers were constructed of nylon fishing line (10 kg breaking strain), secured at one end to a 150 mm long wire staple anchored in the sediment. At the other end, a 25 mm^2 vinyl tab glued to the line provided an attachment point for snails. Prior to tethering, snails were towel dried and their shell heights measured with vernier callipers. They were then glued to the tabs on the fishing line using cyanoacrylate glue gel that was placed on the dorsal surface in the groove between the ultimate and penultimate shell whorls. Artifacts associated with the tethering (see Peterson & Black 1994) were likely minimal given that (1) the tethers were sufficiently long to allow individuals to move and seek refuge from certain predators by climbing pneumatophores (*P. ebeninus* generally travels less than 1 m wk^{-1}, see Bishop et al. 2007b) and (2) pilot studies indicated that predators could still drill, crush and/or drag *P. ebeninus* underground, whether or not they were tethered.

We recorded the fates of tethered *Pyrazus ebeninus* individuals (alive, missing, dead with a shell drilled by predators, dead with a shell crushed by predators, dead with an undamaged shell) 1, 3, 5 and 7 wk after deployment on 31 March 2006 and 26 October 2006. Because none of the size classes was completely depleted by predators in either season, and mortality of snails steadily increased throughout each of the deployment periods, we report only the cumulative mortality over the 7 wk periods. To control for any handling mortality of *P. ebeninus* and to test the durability of the tethers, 3 tethered snails of each size class were placed in each of 3 replicate predator-exclusion cages at each of the 4 sites. The circular cages were 1 m^2 in area and constructed of galvanized 5 mm mesh fences that were 160 mm high and covered with 10 mm light nylon mesh pulled taut across the top. Each cage was held in place with six 450 mm long plastic stakes. Artifacts of caging caused by the alteration of hydrodynamic conditions are likely to be minimal for our cages placed on the mudflat or among pneumatophores (Quibray Bay represents a low-flow environment). Thus we consider the use of cages a reasonable method of quantifying rates of detachment from tethers and mortality due to non-predatory sources.

To test the hypothesis that more small than medium or large *Pyrazus ebeninus* individuals are consumed by predators, we performed fully factorial ANOVAs on $\sqrt{(x + 1)}$ transformed data. These analyses, which utilized the cumulative number of tethered snails consumed per site as replicates, had 3 factors: time of sampling (2 levels: autumn, spring), tidal elevation (2 levels: high, low) and prey size (3 levels: small, medium, large). We analysed each form of predatory mortality (as identified by different forms of shell damage) separately. Prior to each analysis, Cochran's *C*-test was performed to confirm homogeneity of variances. ANOVAs were followed by *a posteriori* Student-Newman-Keuls (SNK) tests to identify pairwise those treatment means that differed significantly at α = 0.05.

Size selectivity by *Conuber sordidus*. Experiments examining size selection by a dominant predator among *Pyrazus ebeninus* size classes were conducted in March and April 2007. These were done using *C. sordidus* which, at our study site, reaches densities of up to 10 m^{-2} (M. J. Bishop unpubl. data). To test

whether *C. sordidus* is size-selective in its predation on *P. ebeninus*, we simultaneously offered 5 small (30.1 to 40.0 mm SH), 5 medium (50.1 to 60.0 mm SH) and 5 large (70.1 to 80.0 mm SH) *P. ebeninus* to a single *C. sordidus* (16.1 to 25.0 mm SH). We chose to place only a single *C. sordidus* within each tank because naticids are known to exhibit aggressive and cannibalistic behaviour towards one another that may interfere with foraging on other species (e.g. Fretter & Manly 1979, Kelley 1991).

In order for the satiation of *Conuber sordidus* in our experiment to accurately reflect the average satiation of this species in the field, both *C. sordidus* and their *Pyrazus ebeninus* prey were hand collected from the Quibray Bay mudflat on the day of experiment set up. Upon collection, snails were transported back to the laboratory and immediately placed together on the sediment surface at the centre of experimental tanks. *C. sordidus* individuals were allowed to feed for 14 d, a period over which pilot studies indicated that sufficient numbers of *P. ebeninus* snails (~25% of the total offered prey) are generally consumed, allowing assessment of any difference in the consumption of differently sized prey. Sampling was not done at intermediate times because naticid gastropods that are interrupted during feeding are not capable of recognizing their own partially completed boreholes to resume drilling over that same location once the prey item is re-encountered (Kitchell et al. 1981, Kingsley-Smith et al. 2003).

During pilot studies we observed that small and medium size *Pyrazus ebeninus* snails placed with *Conuber sordidus* climbed the tank walls, whereas snails of these size classes in tanks without a predator did not. Large *P. ebeninus* individuals did not exhibit this behaviour regardless of whether or not *C. sordidus* was present. To determine whether *P. ebeninus* has a size-dependent escape response to *C. sordidus* and to assess whether this climbing behaviour reduces predatory mortality of size classes that climb walls, we established tanks with and without *C. sordidus*, and (for each predator treatment) with and without cages that inhibited climbing (n = 6 for each treatment). Cages were constructed of weathered 5 mm PVC gutter guard mesh, and extended from the bottom of the tanks to 180 mm above the surface of the sediment. On each day of the 14 d experiment, we recorded the number by size class of snails climbing the walls of each tank and returned these to the sediment surface. After 14 d, aquaria were drained, sediments searched for prey items and the numbers of drilled snails recorded by size class.

For each individual feeding trial, a χ^2 test was done to test for a significant (at α = 0.05) difference in the numbers of each prey type consumed by an individual

Conuber sordidus. Where appropriate, we combined probabilities of independent replicate tests using Fisher's (1954) method. We used χ^2 goodness-of-fit tests to examine whether the proportions of small, medium and large *Pyrazus ebeninus* snails consumed in experiments where climbing was allowed were as predicted from proportions observed in experiments where climbing was inhibited by a cage. Under the null hypothesis of no effect of climbing on size-selectivity by *C. sordidus*, the expected numbers of small, medium and large *P. ebeninus* individuals (E_S, E_M and E_L, respectively) consumed by *C. sordidus* in the treatment where climbing was allowed are:

$$E_S = F_T[C_S/(C_S + C_M + C_L)]$$
$$E_M = F_T[C_M/(C_S + C_M + C_L)]$$
$$E_L = F_T[C_L/(C_S + C_M + C_L)]$$

where C_S, C_M and C_L are, respectively, the numbers of small, medium and large snails consumed when summed across all 6 replicates of treatments in which snails were caged; F_T is the total number of snails consumed across all 6 replicates of the treatment in which they were free to climb. The χ^2 goodness-of-fit test compared these expected numbers with the total numbers of snails consumed in each size class across the 6 replicates in the treatment where they were free to climb (F_S, F_M, F_L for small, medium and large snails, respectively; $F_S + F_M + F_L = F_T$).

Whereas the consumption by some predators of only certain prey items is independent of choice, reflecting stereotypy of behaviour or an inability to successfully consume better defended items within a certain time (Vermeij 1976, Brown & Haight 1992), others display 'preference' (see Underwood et al. 2004), modifying their prey consumption according to prey availability (Elner & Hughes 1978, Davidson 1986). To discriminate between the preferences of *Conuber sordidus* among prey size classes and the greater vulnerability or catchability of certain size classes of *Pyrazus ebeninus*, we compared feeding rates of *C. sordidus* on snails in single size class offerings ('no-choice experiments' sensu Liszka & Underwood 1990) to feeding rates in 'choice experiments' described above. In no-choice experiments, 15 snails of a single size class were offered to a *C. sordidus* individual. To maintain independence, different snails were used in no-choice and choice experiments.

Under the null hypothesis of no preference for one size class over the other, the expected numbers of small, medium and large *Pyrazus ebeninus* specimens consumed by *Conuber sordidus* in choice experiments are:

$$E_S = N_T[M_S/(M_S + M_M + M_L)]$$
$$E_M = N_T[M_M/(M_S + M_M + M_L)]$$
$$E_L = N_T[M_L/(M_S + M_M + M_L)]$$

where M_S, M_M and M_L are, respectively, the numbers of small, medium and large snails consumed when each is presented on its own (in equal numbers) and N_T is the total number of snails consumed when offered together in choice experiments. We estimated M_S, M_M and M_L by summing the number of each size class consumed in no-choice trials across independent replicates. We used χ^2 goodness-of-fit tests to compare these expected numbers with the numbers of snails consumed when presented together (N_S, N_M, N_L for small, medium and large snails, respectively; $N_S + N_M + N_L = N_T$). Because these χ^2 tests are subject to excessive Type I error (see Liszka & Underwood 1990), results were considered statistically significant only when p < 0.01.

Effects of habitat on *Conuber sordidus* predation. To test hypotheses about the role of habitat in influencing predation by *C. sordidus* on small individuals of *Pyrazus ebeninus*, we set up a manipulative field experiment in September 2006. The experiment had 3 factors: height on shore (low and high), site (2 levels: nested within height on shore), and treatment (undisturbed, burial inhibited, structure of vegetation destroyed). At both heights on the shore, we predicted that prey consumption by *C. sordidus,* which drags its prey underground, would be greater in plots where the structure of vegetation is destroyed and burial is allowed than in plots where the structure is destroyed but burial is impeded. On the high shore, where there are pneumatophores (that may decrease foraging efficiency) underlain by a dense network of nutritive *Avicennia marina* roots (that may impede burial), we expected that predation would be greater in disturbed than undisturbed plots. On the low shore, however, where the only vegetation is sparse seagrass, we predicted predation rate to be similar between disturbed and undisturbed treatments.

At each of the 4 sites, we established 15 circular (0.25 m^2) experimental plots, each separated by 2 to 3 m. Plots were randomly allocated to each of the 3 experimental treatments (n = 5). In order to confine snails to manipulated habitat, we erected a galvanized 5 mm mesh fence (of identical construction to the walls of previously described predator exclusion cages) around each plot. All *Pyrazus ebeninus* and *Conuber sordidus* individuals naturally occurring within each plot were removed prior to habitat manipulation. In the 5 plots at each site where burial of snails was to be restricted, we added a 0.25 m^2 circular plate of galvanised 5 mm mesh at a depth of 20 mm below the surface and returned the sediment. At the mid-shore sites, placement of the plate first required pneumatophore removal. Once fitted, the circular plate covered the entire base of the plot. In the 5 plots allocated to root layer destruction, we repeatedly drove a shovel into

the top 300 mm of sediment. Dislodged pneumatophores, mangrove cable roots, and seagrass were then removed from these plots by hand. Undisturbed plots did not receive any treatment.

Following habitat manipulation, we added 10 small (30.1 to 40.0 mm SH) *Pyrazus ebeninus* individuals and a medium-sized (16.1 to 25.0 mm SH) *Conuber sordidus* specimen to each experimental plot. Predators and their prey were left together in experimental plots for a period of 3 wk, after which, each plot was extensively searched for *P. ebeninus* by sieving sediment to a depth of 200 mm. The number of drilled *P. ebeninus* shells was compared among treatments using a 3-factor mixed model ANOVA (tidal elevation: high, low; site: 2 levels nested within each elevation; treatment: no-burial, undisturbed, disturbed).

RESULTS

Field assessments of size-specific predatory mortality

Controls in which tethered *Pyrazus ebeninus* whelks were held in predator exclusion cages indicated no effect of snail handling on non-predatory mortality. In both autumn and spring of 2006, survivorship of snails in predator exclusion cages was 100%. In autumn, when winds averaged 12 knots from the protected south (Australian Bureau of Meteorology, http://www.bom.gov.au/climate/averages/), none of the caged snails detached from their tethers. In spring, however, when winds averaged 16 knots from the northeast (Australian Bureau of Meteorology), 2 of the 12 large snails had detached from their tethers by Week 5, and by Week 7, 10 out of 12 large and 2 out of 12 medium snails had detached. In the open plots, similar size- and season-specific patterns of missing snails were evident, suggesting that unrecovered snails were a result of failure of the tethering glue and not predation. A greater proportion of snails went missing from tethers in spring (43%) than in autumn (18%), and of those missing in spring, 41% were large and 35% were medium sized. Thus, only damaged snails are considered as evidence of predation. Damaged snails could be divided into those that were drilled (characterised by the presence of a parabolic hole on the penultimate whorl of the ventral side) and those that were cracked (where only fragments of the shell remained attached to the tether). Of the 2 forms of mortality, drilling was the more prevalent, affecting 4% of *P. ebeninus* shells in the autumn and 11% in the spring (cf. 3% of snails cracked during each deployment period).

Across both seasons and heights on the shore, significantly more small than medium or large *Pyrazus*

ebeninus specimens were drilled over the 7 wk deployment period (ANOVA: main effect of size, $F_{2,12}$ = 7.11, p = 0.009; Fig. 1). Whereas drilled small snails were detected at all tidal elevations in autumn and spring, no medium or large snails were drilled on the low shore in autumn, and a single snail in each of these size classes was drilled on the high shore only. In spring, no large snails were drilled at any of the sites and drilling of medium snails was confined to the low shore. Although more small snails were drilled on the high than the low shore, and overall mortality due to drilling was greater in spring than autumn, these patterns were not statistically significant (ANOVA: height by site interaction, $F_{2,12}$ = 3.5, p = 0.064; main effect of season, $F_{1,12}$ = 4.13, p = 0.065).

Patterns in the proportion of *Pyrazus ebeninus* shells that were cracked (as opposed to drilled) were more time and location specific (ANOVA: season by height by size interaction, $F_{2,12}$ = 18.91, p < 0.001; Fig. 1). Whereas cracked snails were observed only at high shore sites during autumn, cracking of shells was confined to low shore sites in spring. As with drilling, shell cracking followed a size-specific pattern, with more small than medium or large snails succumbing to this form of predation. Indeed, in spring only small snails experienced cracking. Medium and large snails were cracked at high shore sites in autumn, although these proportions were lower than for small snails.

Size selectivity by *Conuber sordidus*

Counts of numbers of *Pyrazus ebeninus* individuals climbing the walls of aquaria confirmed observations from pilot studies that small and medium snails display an escape response to the predator *Conuber sordidus.* Much higher numbers of climbing snails were observed in treatments with than without *C. sordidus* (Fig. 2). Of the snails observed climbing, the greatest number came from the medium size class. While small snails also climbed, not one large specimen was found on the walls of the aquaria over the experimental period.

As in field experiments, laboratory experiments revealed a strong effect of prey size on the susceptibility of *Pyrazus ebeninus* to predation. Of the 12 independent trials in which an individual *Conuber sordidus* specimen was offered all 3 size classes of *P. ebeninus* (6 with and 6 without cages that prevented a climbing escape-response), significant size electivity was detected in 5 (Table 1). When p-values from independent trials of each treatment were combined, a highly significant effect of prey size on *P. ebeninus* mortality was found regardless of whether or not the snails were allowed to exhibit escape responses. This result could be attributed to the consumption of more small than medium individuals and the absence of predation upon large *P. ebeninus* specimens (Table 1). Summing all replicate trials in which cages prevented climbing showed that consumption of small whelks was double that of medium individuals; when snails were allowed to climb, consumption rate on small snails was almost 5 times greater than that on medium specimens (Table 1). However, despite the general trend for a smaller contribution of medium-sized snails to total prey consumed when an escape response was allowed than when it was inhibited by a cage, caging was not found to have any significant effect on the contribution of snail size classes to total prey consumed (χ^2 goodness-of-fit test, p = 0.09). Controls without *C. sordidus* indicated negligible prey mortality in the absence of the predator.

There was no effect of choice on the percentage contribution of each of the 3 size classes of *Pyrazus ebeninus* to total prey consumed by *Conuber sordidus* (χ^2 goodness-of-fit test, p = 0.78). The 73% contribution of small snails and the 27% contribution of medium snails to total prey consumed in no-choice
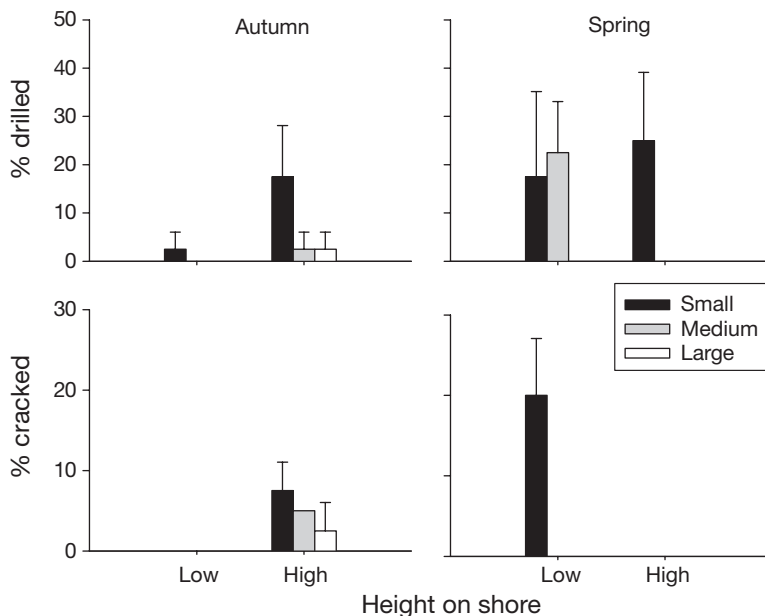

Fig. 1. *Pyrazus ebeninus*. Mean (+SE) percentage of small (30.1–40.0 mm shell-height, SH), medium (50.1–60.0 mm SH) and large (70.1–80.0 mm SH) snails that were drilled or cracked at the end of 7 wk experimental periods in autumn and spring. n = 2 sites at each of 2 tidal heights considered
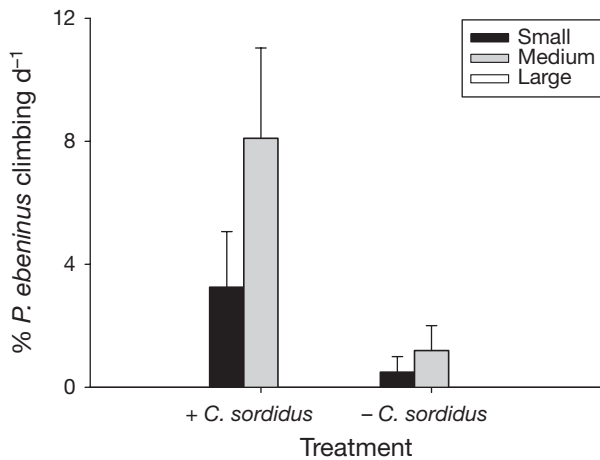
Fig. 2. *Pyrazus ebeninus*. Mean (+SE) percentage of small (30.1 to 40.0 mm shell-height, SH), medium (50.1 to 60.0 mm SH) and large (70.1 to 80.0 mm SH) snails found each day climbing the walls of tanks with (+) and without (–) the predator *Conuber sordidus* (n = 6 replicate tanks). *P.*: *Pyrazus*, *C.*: *Conuber*

experiments compared closely to the 67 % contribution of small snails and 33 % contribution of medium snails in treatments where the 3 size classes were offered to predators simultaneously. No large *P. ebeninus* individuals were consumed over the 14 d period, even when alternative size classes of prey were absent from aquaria.

Effects of habitat on *Conuber sordidus* predation

Experimental manipulations failed to produce any evidence for a role of habitat in mediating effects of *Conuber sordidus* predation. Single *C. sordidus* specimens placed with 10 small *Pyrazus ebeninus* snails consumed similar numbers of this prey item over a 3 wk period regardless of whether or not (1) burial was

prevented by the presence of a galvanised mesh plate (3.0 ± 0.7 snails consumed [mean ± SE]), (2) the structural integrity of the sedimentary environment was maintained (3.9 ± 0.6 consumed), and (3) the sediment was disturbed and structural elements of aquatic vegetation removed (4.1 ± 0.9 consumed; ANOVA: no main treatment effect, $F_{2,4} = 0.67$, p = 0.561). Prey consumption did not differ detectably between plots on the high and low shore (ANOVA: no main tidal elevation effect, $F_{1,2} = 2.32$, p = 0.268).

DISCUSSION

Within populations of detritivorous trophic cul-de-sacs, it is presumably the larger individuals that interfere most with the transfer of carbon from detritus to higher trophic levels. In moving across the landscape, large individuals cause the greatest physical disturbance of sediments, dislodging other macroinvertebrates that are critical to efficient trophic transfer, and interfering with their feeding, reproduction and/or settlement (Curtis & Hurd 1979, Feller 1984, Dunn et al. 1999). Furthermore, in ingesting greater volumes of sediment than smaller individuals, large detritivores display greater potential to deplete food resources. However, despite the primary role of larger individuals in directly and indirectly driving resource depletion, smaller individuals may (through their susceptibility to predation) be the ultimate determinants of the strength of the trophic cul-de-sac, governing the amount of carbon that is 'leaked' up to higher trophic levels. Although the present study, like previous work (Bishop et al. 2007a), demonstrated resistance of large *Pyrazus ebeninus* snails to predation, our finding that smaller specimens are, by contrast, subject to considerable predatory mortality has important implications in interpreting the role of *P. ebeninus* as a trophic cul-de-sac.

Table 1. *Pyrazus ebeninus*. Mortality over a 14 d period of small (S: 30.1 to 40.0 mm shell-height, SH), medium (M: 50.1 to 60.0 mm SH) and large (L: 70.1 to 80.0 mm SH) individuals in aquaria with (+) and without (–) the predatory gastropod *Conuber sordidus*, and with and without cages that prevented prey from climbing the walls. Five *P. ebeninus* specimens of each size class were placed in each aquarium, giving a total of 30 specimens of each size class across the 6 replicates of each treatment. The χ^2 statistic tested for a significant difference in mortality among the 3 size classes of *P. ebeninus*. Drill holes characteristic of *C. sordidus* predation were evident among all dead prey except those in the cage control lacking a predator. n = 6 independent trials for each treatment

Treatment	Total *P. ebeninus* mortality			Outcomes of n independent χ^2 tests			Fisher's combined probability	
	S	M	L	p > 0.05	p < 0.05	p < 0.01	χ^2	p
+ *C. sordidus*, + cage	18	9	0	4	1	1	29.7	0.003
+ *C. sordidus*, – cage	19	4	0	3	2	1	37.0	<0.001
– *C. sordidus*, + cage	0	1	1					
– *C. sordidus*, – cage	0	0	0					

Whereas only 2 out of 160 large *Pyrazus ebeninus* specimens suffered predatory mortality during field deployments of tethered snails, small individuals (30.1 to 40.0 mm SH) were preyed upon consistently across all habitats and seasons. Predation on smaller snails may be attributable to at least 2 types of predator: naticid gastropods that bore holes in their molluscan prey and predators that crush their prey (perhaps elasmobranchs, toadfish or crabs). On average, 21% of small tethered *P. ebeninus* specimens were drilled and 4% crushed over a 7 wk period. Medium size snails (50.1–60.0 mm SH) experienced predation rates that were intermediate between those of the other 2 size classes; on average 2.5% were drilled and 5% crushed over a 7 wk period; death by predation in the medium size class was notably absent from some sites in certain seasons.

Whether this observed predation on small *Pyrazus ebeninus* snails should be viewed as a 'leak' in the cul-de-sac or rather as a facilitator that focuses predation away from the large size classes that cause greatest damage will, however, depend on the mechanism by which the predation occurs. Differences among size classes in susceptibility to predation may reflect (1) predator preferences for particular prey sizes (Elner & Hughes 1978, Davidson 1986), (2) stereotypy of predator behaviour (Hughes 1985), or (3) prey species ontogenetic change in anti-predator defence leading to greater consumption of the most vulnerable prey size classes by non-selective predators (Vermeij 1976, Brown & Haight 1992). Thus, although common benthic predators may be incapable of eating large *P. ebeninus* individuals, it may also be the case that they would consume the large snails were they given no choice among prey size classes, but when presented with an array of prey sizes, they would consume smaller rather than larger prey items. Laboratory experiments comparing prey consumption by the naticid gastropod *Conuber sordidus*, an abundant predator at our study site, under choice and no-choice experimental configurations indicated that greater susceptibility of small than medium or large individuals of *P. ebeninus* may not be attributed to predator preference. Even in the absence of small prey items, larger *P. ebeninus* specimens were not consumed, suggesting that consumption of the small *P. ebeninus* should be viewed as a leak, not a facilitator of the cul-de-sac. Quantifications of (1) prey encounter rates, (2) persistence and (3) handling times were not attempted due to difficulties in making the measurements in a 3-dimensional sedimentary environment. Possible, but untested, explanations for the decreasing susceptibility of *P. ebeninus* to *C. sordidus* predation with increasing prey size may, however, be that (1) the much thicker shell of large prey snails is impenetrable for

most *C. sordidus* individuals, (2) large *P. ebeninus* snails have a greater ability than smaller conspecifics to escape when attacked and/or (3) *C. sordidus* has stereotypy of behaviour (always declines predation on large prey even in the absence of smaller prey types [possibly because of elevated energy consumption during handling of large prey items]).

Predation by *Conuber sordidus* on *Pyrazus ebeninus* was independent of habitat structure. When single *C. sordidus* specimens were enclosed with 10 small *P. ebeninus* snails, similar numbers of prey were consumed, regardless of whether or not the predator was prevented from burrowing by (1) means of a mesh plate buried 20 mm below the surface of the sediment, (2) pneumatophores up which the prey may climb to escape, or (3) a dense root mat that decreased penetrability of the sediment. Despite differences in the predatory mortality rate of tethered *P. ebeninus* specimens between low and high shore sites open to predators, similar rates of predation occurred across tidal elevations in the experimental manipulation habitat. This suggests that across-elevation mortality differences in tethered snails were driven by differences in predator abundance (a factor that was held constant in the experimental manipulation habitat) and not differences in the habitat itself. Our failure in the manipulative experiment to detect effects of habitat on predation rate is consistent with results of the laboratory experiment. In the laboratory, no difference in predatory mortality was seen between experimental treatments allowing or preventing snail climbing to escape predators.

From what is now known, we can propose that the trophic cul-de-sac provided by fully grown snails would persist despite predation on small *Pyrazus ebeninus* individuals. Firstly, the high frequencies of large snails in populations across all habitats (M. J. Bishop unpubl. data) suggest that predation on small specimens does not prevent snails from recruiting in significant numbers to the larger damage-causing size classes. Secondly, the high degree of spatial segregation between small and large snails at our study site suggests that the predators feeding on small snails in the mangrove forest are likely not the species of birds and fish that feed on mudflat invertebrates at low tide; these birds and fish are affected by the low-shore carbon depletion caused by large individuals of *P. ebeninus*. Thus, even if there were significant trophic transfer by small *P. ebeninus* snails in the mangrove stands, a trophic cul-de-sac caused by adult *P. ebeninus* could operate on the mudflat. Finally, because those size classes of *P. ebeninus* that drive resource depletion experience little predatory mortality, trophic transfer by smaller individuals likely has little effect on the strength of the trophic cul-de-sac. Following the establishment of the Exuma Cays Land

and Sea Park, Bahamas, the restoration of piscivore biomass did not significantly decrease grazing by parrotfish on the reef because large-bodied parrotfish (which are responsible for the bulk of grazing) were able to escape predation and increased in abundance due to reductions in fishing pressure (Mumby et al. 2006). Rather than weakening the trophic cul-de-sac, predation on small *P. ebeninus* individuals may ensure that populations continue to be dominated by the large, damage-causing size classes.

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