Ecology Letters, (2005) **8**: 160–166 doi: 10.1111/j.1461-0248.2004.00700.x

LETTER

As good as dead? Sublethal predation facilitates lethal predation on an intertidal clam

John J. Meyer* and James E. Byers
Department of Zoology, University of New Hampshire, 46 College Road, Durham, NH 03824, USA
**Corresponding: E-mail: jjmeyer@unh.edu*

Abstract

Although ecologists have speculated that sublethal predation can impact prey dynamics, consequences of these predator effects have seldom been experimentally tested. In soft-sediment marine communities, fishes crop extended feeding siphons of buried clams, potentially causing clams to reduce their burial depth, thereby enhancing their susceptibility to excavating lethal predators. We simulated cropping of the confamilial clams, *Protothaca staminea* and *Venerupis philippinarum*, by removing the top 40% of siphons, which caused each species to burrow 33–50% shallower than conspecifics with intact siphons. To examine subsequent consequences of reduced burial depth, we exposed cropped and intact clams to natural levels of predation in the field. Because of a naturally longer siphon, *Protothaca*, even after cropping, remained at relatively safe burial depths. In contrast, siphon cropping nearly doubled the mortality rate of *Venerupis*. Thus, while sublethal predation facilitates lethal predation, this linkage depends on specific life history characteristics, even among ecologically similar species.

Keywords

Behavioural modification, facultative commensalism, predator avoidance strategies, predator facilitation, prey refuge, risk enhancement, siphon nipping, soft sediment communities, trait-mediated effects.

Ecology Letters (2005) 8: 160–166

INTRODUCTION

Although predation is recognized as a key factor that structures natural communities, how predator effects combine synergistically to affect prey populations has only recently been rigorously explored (Sih *et al.* 1998). Studies of multiple predator effects have typically found that competition and general interference among predators results in risk reduction for shared prey (e.g. Huang & Sih 1991; Rosenheim *et al.* 1993). Less commonly, risk enhancement for shared prey may result due to facilitation among predators (Kerfoot & Sih 1987; Korpimäki *et al.* 1996; Losey & Denno 1998). Predominantly risk enhancement has been documented when one predator induces a change in behaviour or habitat use of a shared prey species that positively benefits a second predator, for example, when a prey evades one predator but consequently exposes itself to another (Kotler *et al.* 1993; Soluk 1993). However, a predator that merely alters prey behaviour or habitat use may receive little or no benefit itself. A form of risk enhancement that allows both predators to benefit occurs if sublethal predation by one predator facilitates the rate of lethal predation by another.

While common among plants, sublethal predation also occurs among animals, particularly among taxa known for regenerative abilities and autotomy (de Vlas 1979; Bowmer & Keegan 1983; Dial & Fitzpatrick 1984; Lindsay & Woodin 1992; Lindsay *et al.* 1996; Sasaki *et al.* 2002). However, few examples clearly demonstrate a definitive facilitative link between sublethal predation and enhanced lethal predation. Dial & Fitzpatrick (1984) in a laboratory experiment demonstrated that lizards without tails (experimentally removed to simulate sublethal predation) suffered 100% mortality from snakes compared with 27% for lizards with intact tails. Mouritsen (2004) showed that cockles moving across the sediment surface often lose foot tissue to sublethal predation by fish. This renders the bivalve unable to burrow, increasing its vulnerability to predation by shorebirds and predatory whelks until its foot has regenerated. Although sublethal predation allows a prey to survive an encounter with the predator, physical damage sustained by the prey may enhance its vulnerability to a subsequent lethal predator.

Sublethal predation on burrowing bivalves occurs when fish, shrimp, and sometimes crabs clip a portion of the

clam's soft-tissue, generally the siphon, without causing mortality (de Vlas 1979; Peterson & Quammen 1982; Kamermans & Huitema 1994; Smith *et al.* 1999; Sasaki *et al.* 2002). Although most clams have hard shells, their most effective defense against lethal predators is burial within the sediment which decreases detection by predators and increases predator handling costs (Virnstein 1977; Blundon & Kennedy 1982; Zaklan & Ydenburg 1997; Smith *et al.* 1999; Seitz *et al.* 2001). Shallowly buried clams are in general more susceptible to excavating lethal predators (Haddon *et al.* 1987; Smith *et al.* 1999; Whitlow *et al.* 2003). While burial depth can be affected by habitat characteristics (Seitz *et al.* 2001, 2003; Tallqvist 2001; Byers 2002), siphon length and siphon biomass generally dictate the maximum burial depth of a clam (Zwarts & Wanink 1989; Zwarts *et al.* 1994; de Goeij *et al.* 2001). Because a clam's siphon must reach the water column to extract necessary food and oxygen, clams with siphons shortened by cropping may be forced to move closer to the sediment surface to compensate until the siphon has regenerated. Several direct costs associated with siphon cropping have been examined, including reduced growth and reproductive ability (Coen & Heck 1991; Kamermans & Huitema 1994; Irlandi & Mehlich 1996). However, it has only been suggested that siphon cropping may in fact facilitate lethal predation (Hodgson 1982; Zwarts 1986; Skilleter & Peterson 1994; de Goeij *et al.* 2001). In this study, we explicitly test and quantify the linkage.

Study system

Several fish species in the north-eastern Pacific, including sole, flounder, and sculpin species crop siphons as a foraging technique (Miller 1967; Armstrong *et al.* 1995). Potential bivalve prey include the confamilial burrowing clams, *Protothaca staminea* and *Venerupis philippinarum* (Family: Veneridae), common on intertidal beaches. *Protothaca* (Pacific littleneck clam) is native to north-eastern Pacific shores and co-occurs with *Venerupis* (Asian littleneck; Manila clam), a non-indigenous species that has been well established throughout the Pacific Northwest for > 50 years (Byers 2005). These clams are morphologically and ecologically similar, overlapping in their spatial distributions and habitat requirements. Both species can live up to *c.* 10 years (Emmett *et al.* 1991). Both feed by filtering particles from the water column through siphons that extend to the sediment surface, leaving them susceptible to siphon cropping. Although similar in many ecological and life history attributes, one distinguishing characteristic is that for a given size, *Protothaca* burrows 2–4 cm deeper than *Venerupis* (Haderlie & Abbott 1980, Byers 2005).

Lethal clam predators primarily include the three regionally abundant *Cancer* crabs – *Cancer magister* (Dungeness crab), *C. gracilis* (graceful crab), and especially *C. productus* (red rock crab) – all of which are common in the shallow subtidal and intertidal of the north-eastern Pacific. Crabs detect bivalve prey through chemical cues and odours, locating siphons and siphon holes, and by using their pereopods to assess clam depth (Smith *et al.* 1999). Crabs then excavate their prey and use their chelae to crack the clam's shell and access the tissue inside.

Using a field survey on San Juan Island, WA, USA we established that conservatively 10% of both *Protothaca* and *Venerupis* exhibit cropped siphons at any given point in time. (Only clams exhibiting differences in siphon length, morphology, *and* colour were scored as cropped in our estimate.) Additionally, we collected two documented siphon cropping fish species [*Leptocottus armatus* (Pacific staghorn sculpin), $n = 12$; *Myoxocephalus polyacanthocephalus* (great sculpin), $n = 16$] and found clam siphons in 25 and 31% of their stomachs, respectively. Our goal is to determine whether such siphon loss subsequently increases the vulnerability of each clam species to lethal predators. We predict that sublethal predation by siphon cropping fish will force clams to decrease their burial depth, in turn increasing the likelihood of lethal predation by excavating crabs. However, we hypothesize that the relative effects on the two clams should differ as a function of their natural differences in burial depth, with siphon nipping affecting shallowly burrowing clams more severely.

MATERIALS AND METHODS

Clam burial depth

We initiated a laboratory experiment to determine how clam burrowing depths depend on species and siphon condition (intact or cropped). Because siphons scale with clam body size within each clam species (as quantified in the following section), we standardized the size of clams used in our study [mean length (mm) ± SD; *Protothaca*: 47.8 ± 2.7; *Venerupis*: 46.0 ± 3.0]. Experimental clams were placed into buckets with non-circulating seawater and after several hours the clams extended their siphons and began to feed allowing us to crop siphons with stainless steel surgical scissors. From 28 clams of each species we haphazardly selected half to serve as unmanipulated clams with intact siphons. From the remaining half we removed the top 40% of siphon, an amount consistent with the proportion of siphon missing from cropped clams in our field survey. All cropped portions of siphon were dried and weighed to quantify the amount of siphon biomass removed. Specifically, by comparing the removed portion of the siphon to the expected total siphon weight estimated from regression of siphon dry weight vs. clam length, we calculated the proportion of siphon removed from each clam (and by

subtraction, the proportion remaining). We chose to quantify siphon mass (as discussed in the following section) instead of siphon length because of higher error associated with measuring length; in general, the two variables are well correlated (Zwarts *et al.* 1994).

Cropped and intact clams of both species ($n = 14$ for each species × siphon condition treatment) were haphazardly scattered into seatables (120 × 40 × 45 cm) containing sand and gravel sediment 17 cm deep that was collected from Argyle Lagoon on San Juan Island, WA, USA (the site of fish surveys and our field study described below). Unfiltered seawater circulated throughout each seatable and emptied via a standing drain pipe that controlled water depth at 25 cm. We oriented each clam with its foot down and pushed each animal approximately one-half of its shell length into the sediment, after which it was allowed to burrow autonomously. After 6 days, each clam's depth was carefully measured to the nearest 0.1 cm with a ruler and then excavated from the sediment. In a second, consecutive trial we repeated the entire experimental procedure with new clams. Because no temporal differences were found in burial responses, data from the two trials were pooled for analyses (total $n = 28$ clams per siphon treatment per species).

Burial depths of the clams were compared with a two-way ANOVA treating species and siphon treatment (intact vs. cropped) as fixed factors. To document how tightly siphon biomass controls clam burial depth across species and siphon conditions, we regressed burial depth for all experimental clams against siphon mass.

Siphon investment

To help explain observed species specific differences in burial depth and to quantify the amounts of siphon removed for burial depth trials, we examined siphon investment for the two clam species. Specifically, we quantified how siphon biomass varies with clam size by constructing relationships between siphon biomass and clam length. We haphazardly selected *c.* 60 adult clams of each species across a large size range (*Protothaca* length: 28.7–58.8 mm; *Venerupis* length: 23.2–56.8 mm). Clams were frozen at −20 °C for 24 h prior to dissection. After clams were thawed and measured, all tissue was removed from the shell using a scalpel and forceps, and siphons were separated from the main body of tissue. The clam's siphon and remaining soft-body tissue were separated into two pre-weighed aluminium pans, dried for 12 h at 75 °C, and weighed to the nearest 0.0001 g. ANCOVA was used to compare differences between the siphon biomass (ln transformed) of the two species with clam size as the covariate. In the absence of a significant species × clam size interaction term, the adjusted least square means for each species were compared to quantify the difference in siphon biomass for an average sized clam.

Lethal predation experiment

To test if clams become more vulnerable to lethal predators after siphon cropping, we manipulated clam species and siphon condition in a two-factor field experiment that exposed all clams to natural predator densities. We manually cropped clam siphons using the same protocol and the same clam size class (range 40–49 mm) employed for the burial experiment. Clams were individually measured and marked with permanent black ink. To ensure cropping *per se* did not cause any immediate mortality that would confound interpretation of the field experiment, clams were held for 24 h in laboratory seatables. Also we cropped the siphons of 30 control clams of each species and held these in seawater tanks in the laboratory during the duration of the field experiment.

At low tide on 13 November 2003, we established the +0.5 m mean lower low water (MLLW) tidal height at Argyle Lagoon and placed 24 enclosures into the sediment separated by *c.* 30 cm and running parallel to the waterline. Enclosures (0.3×0.3 m $= 0.09$ m^2) were constructed of 1.25 cm-mesh hardware cloth and inserted *c.* 17 cm into excavated holes in the substrate. This depth extended well beyond the typical natural burial depth of each clam species (Haderlie & Abbott 1980; Byers 2005). The excavated sediment was then used to fill the enclosures, after which each enclosure received 12 clams of a single species and siphon treatment. This number of clams represents realistic ambient biomass of these species (Byers 2005) and also provided acceptable resolution for quantifying clam mortality. Each treatment (species × siphon condition) was replicated six times, and to ensure adequate interspersion of treatments we used a randomized block design. Clams were left to burrow autonomously, therefore hardware cloth tops were fastened over the enclosures to remove the initial threat of predation. After 4 days, no clams were visible on the sediment's surface, and all tops were removed from the enclosures.

On four occasions during the experiment, we returned to the site to scour the beach and collect the remains of any killed experimental clams. All clam shells that were recovered were determined to be killed by crabs based on the condition of the shell (e.g. chipped and cracked valves). Bird predators were never observed in the vicinity of the cages. The experiment was terminated after 29 days and the sediment in each enclosure was excavated and sieved to recover experimental clams. Several clams were unaccounted for, i.e. absent from the cage with no trace of cracked shell in the immediate area. Because the enclosures inhibited clam emigration, we assumed that missing clams were removed from the enclosure by a predator. Mortality proportions within each enclosure were Anscombe transformed to normalize their distributions for statistical

analyses (Zar 1996) and compared using a two-way ANOVA with species and siphon condition as fixed factors.

RESULTS

Clam burial depth

In the laboratory, *Protothaca* with intact siphons burrowed to an average depth of 6.8 ± 0.4 cm (mean ± SE), whereas with cropped siphons they attained a shallower depth of 4.0 ± 0.3 cm (Fig. 1). *Venerupis* with intact siphons burrowed to 2.9 ± 0.2 cm, and with cropped siphons burrowed to 1.3 ± 0.2 cm (Fig. 1). Overall, species, siphon condition, and their interaction significantly affected burial depth (ANOVA: species × siphon treatment interaction, $F_{1,108} = 4.7$, $P = 0.033$). Across species and siphon treatments, siphon weight explained 50% of the overall variability in burial depth (Fig. 2).

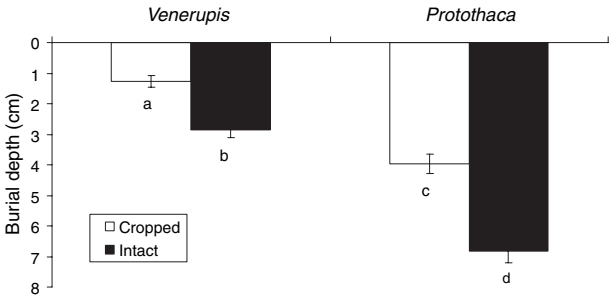

Figure 1 Burial depth (cm) of each clam species as a function of siphon treatment (cropped or intact). Error bars represent 1 SE. Different letters above bars denote groups identified as significantly different by Tukey *post-hoc* analyses.

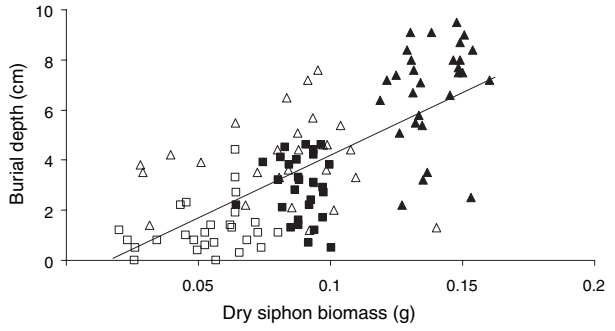

Figure 2 Burial depth as a function of estimated siphon dry biomass for *Venerupis* (squares) and *Protothaca* (triangles). Also depicted are the different siphon treatments: cropped (open symbols) and intact (closed symbols). All clams form a single relationship ($R^2 = 0.50$, $P < 0.0001$). For adult clams, assuming the radius of the siphon changes little relative to length as the siphon grows, increases in siphon biomass should scale approximately linearly with length (and burial depth).

Siphon investment

Clam length correlated positively with siphon dry tissue mass of both species (*Protothaca* $R^2 = 0.68$, *Venerupis* $R^2 = 0.67$). The interaction of species and clam size on siphon mass was marginally significant (ANCOVA: $F_{1,119} = 3.69$, $P = 0.06$). The separate effects of species and size on siphon mass were both significant (species: $F_{1,119} = 12.74$, $P = 0.0005$; size: $F_{1,119} = 233.4$, $P = 0.0001$). On average *Protothaca* had 59% more siphon biomass than *Venerupis* – a difference consistent across all clam sizes. Additionally, *Protothaca*'s siphon mass relative to total body mass (7.6%) was also consistently larger than *Venerupis* (5.6%) (ANOVA on arcsin square root transformed proportions: $F_{1,121} = 4.49$, $P = 0.036$).

Lethal predation experiment

There was a significant interaction effect between species and siphon condition, reflecting that siphon cropping increased mortality in *Venerupis* but had no significant effect on *Protothaca* (ANOVA: $F_{1,20} = 4.69$, $P = 0.043$; Fig. 3). Specifically, over the course of a month, *Protothaca* with intact and cropped siphons had similar, moderate mortality rates [intact: 0.26 ± 0.06 (proportion dead per enclosure ± SE); cropped: 0.19 ± 0.03]. *Venerupis*' mortality, however, was significantly higher and was affected significantly by siphon treatment. *Venerupis*' mortality rate was 0.38 ± 0.05 for clams with intact siphons and 0.60 ± 0.11 for siphon-cropped individuals (Fig. 3). Thus, even with cropped siphons, *Protothaca*'s mortality rate was less than *Venerupis* with intact siphons. None of the mortality was attributable to the cropping procedure *per se*, as none of the cropped control clams held in sediment in the laboratory seawater tables died during the course of the field experiment.

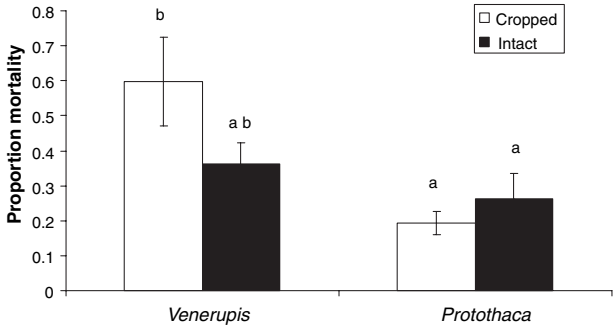

Figure 3 Mortality of *Protothaca* and *Venerupis* in the lethal predation field experiment. Intact clams depicted with solid bars, cropped clams with open bars. Error bars represent 1 SE. Different letters above bars denote groups identified as significantly different by Tukey *post-hoc* analyses.

After the month-long field trial, clams of both species were regenerating siphon tissue and had not yet developed black distal tips characteristic of uncropped or fully regenerated clams. All experimentally cropped clams exhibited orange coloration at the siphon end and none had regenerated more than 65% of their lost siphon biomass.

DISCUSSION

Venerupis mortality nearly doubled when their siphons were experimentally cropped, demonstrating that sublethal predation (siphon-cropping) can facilitate lethal predation. Because siphon biomass in the amounts naturally and experimentally cropped requires several weeks to regenerate, clams must compensate in the interim by moving closer to the sediment surface. While reductions of siphon biomass did cause both clams to decrease their burial depths, only *Venerupis* relocated shallowly enough to be more readily detected and excavated by crab predators. In contrast, *Protothaca* naturally resides twice as deep in the sediments as *Venerupis*. Even cropped *Protothaca* that have adjusted their burial depth are still deeper than intact *Venerupis*.

Burial depth across both species is largely a function of siphon investment. For example, *Protothaca* for a given size maintains a higher siphon biomass and allocates a higher percentage of its total tissue biomass to siphon development than does *Venerupis*. Consequently, *Protothaca* achieves deeper burial – a key element in determining how siphon cropping affects mortality. Therefore, compared with *Venerupis*, *Protothaca* is less vulnerable to siphon cropping because it typically can still remain relatively deeply buried within the sediment. Equivalent mortality rates of intact and cropped *Protothaca* suggest that *c.* 4 cm may be a threshold depth that these venerid clams must achieve to remain relatively unaffected by excavating predators (Fig. 4). Given similar cracking resistance of *Protothaca* and *Venerupis*' shells (J.E. Byers, unpublished data), we predict that if enough siphon biomass were cropped to cause *Protothaca* to cross this threshold, its mortality from crabs and probing predators would similarly increase.

Predator handling time increases dramatically for deeper clams due to increased search time and excavation (Smith *et al.* 1999; Seitz *et al.* 2001). However, while deeper burial depth does reduce *Protothaca*'s risk of predation, there are energetic costs associated with greater burrowing depths. Specifically, deeper clams like *Protothaca* can grow up to six times slower than *Venerupis* (Byers 2005). This reduced growth stems from deeper clams having higher investment in siphon tissue and lower feeding rates by transporting food over a longer distance (Zaklan & Ydenberg 1997). Thus, *Venerupis*' risk of predation from being shallower is partially mitigated by faster growth that allows the clams to achieve higher age-specific fecundity (Byers 2005), and

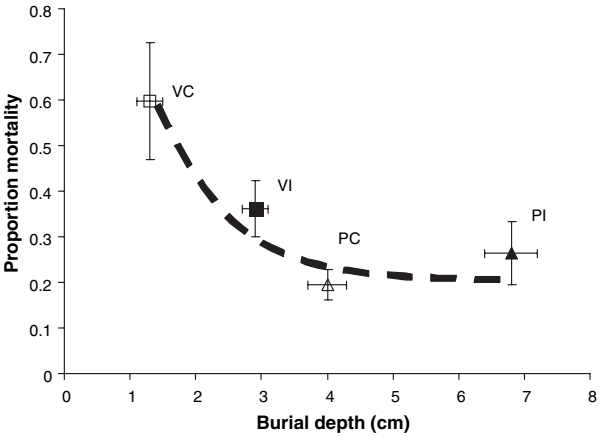

Figure 4 Mortality of each clam species and siphon cropping treatment as a function of burial depth. VC, *Venerupis* cropped; VI, *Venerupis* intact; PC, *Protothaca* cropped; PI, *Protothaca* intact; also symbols are the same as Fig. 2. Dashed line is drawn by hand to suggest a potential asymptote of mortality rate at a threshold burial depth of *c.* 4 cm. Error bars represent 1 SE.

possibly more quickly reach an ultimate size refuge from crab predation (Boulding 1984). Life history evolution may select for the appropriate species-specific balance of the growth-mortality tradeoff that burial depth largely controls. Also the differential responses of the clam species suggest that *Venerupis* abundance will correlate more strongly and negatively with predator abundance.

Rates of predation on clams in the field experiment, including clams with intact siphons, were slightly higher than natural rates and may have been caused by at least two possibilities. One explanation is that the excavation of sediment to implant enclosures loosened the normally packed sediment and allowed easier penetration by excavating crabs. Also, although we used experimental densities realistic for the region, they were slightly elevated for this particular beach at Argyle, and denser aggregations of clams may have attracted predators. However, we were focused on quantifying and comparing the relative mortality differences between the species and siphon conditions and the degree to which sublethal predation enhances vulnerability to lethal predators.

In fact, our study likely underestimates the natural occurrence of sublethal facilitation of lethal predation by manifesting at least two conservative biases. First, our field snapshot estimates of siphon cropping occurrence do not capture clams killed quickly after cropping – a bias that may be particularly pronounced in *Venerupis*. Second, lethal predators benefit not only from reduced burial depths of clam prey, but also from olfactory scents or related cues that are likely released when siphons are cropped that aid in their discovery. Predators in our experiment had less time to

benefit from these cues since lethal predators were not given access to experimental clams for 5 days after cropping, providing time for open wounds to begin healing and odours from cut tissue to dissipate (Hodgson 1982).

Although crabs may sometimes crop siphons themselves (Smith *et al.* 1999), in turn facilitating their own lethal predation of clams, the facilitative link is likely to remain largely dependent on fish in this system. *Cancer* crabs appear to be disadvantaged when it comes to sublethal predatory tactics because they often use tactile cues to detect their prey, affording clams the opportunity to retract and protect their siphon (Smith *et al.* 1999). Fish, on the other hand, can glide near an extended siphon and then strike at the unsuspecting prey. Additionally, crabs probably lack strong selective pressures to improve their cropping ability. For example, crabs already find and consume non-cropped clams. Also, as an opportunistic generalist predator, a crab experiences only diffuse selective pressures from any one prey. Even if selective pressures were present, crabs may be physiologically constrained to respond with the measures that siphon cropping requires. For example, while the claw of durophagous *Cancer* crabs has been shaped for multiple uses, the primary one, i.e. crushing strong material, may be incompatible with nimble requirements for siphon cropping (Smith *et al.* 1999; Taylor 2000). Ultimately, constraints on crab siphon cropping abilities likely serve to maintain the evolutionary stability of the facultative fish-crab interaction.

Clams that lose siphon mass are often as good as dead, but only if sufficient mass is lost to force them shallower than a critical threshold burial depth. However, even closely related prey species may be differentially affected by facilitation among predators depending on the details of their natural history. The interplay of sublethal and lethal predation on *Venerupis* is a striking example of predator facilitation. Specifically, sublethal siphon cropping by fishes has a negligible direct effect on clam mortality; however, its sizable indirect effect on *Venerupis* mortality underscores how synergism between multiple predators can dramatically affect prey populations. Although seldom explored empirically, predator facilitation of this sort may be common in nature given the number of taxa that experience sublethal predation. It may also be common because prey are rendered more vulnerable through physical modification, and not through variable, context-dependent behaviour that underlies most current examples of facilitation among predators.

ACKNOWLEDGEMENTS

Thanks to M. Baltzley, E. Brand, S. Clayman, A. Glaub, A. Newsom, F. Oyarzun, C. Ruben, A. Salomon, J. Selgrath, T. Storr, and M. Toran for effort in the field. M. Billington, J. Gregg, D. Gunderson, J. Kido, and B. Miller were instrumental in the early stages of this project. G. Belovsky, J. Grabowski, M. Vos, and two anonymous refereers helped refine the manuscript. Friday Harbor Labs at the University of Washington provided laboratory space and resources.

REFERENCES

Armstrong, J.L., Armstrong, D.A. & Mathews, S.B. (1995). Food habits of estuarine staghorn sculpin, *Leptocottus armatus*, with focus on consumption of Dungeness crab, *Cancer magister*. *Fish. Bull.*, 93, 456–470.

Blundon, J.A. & Kennedy, V.S. (1982). Refuges for infaunal bivalves from blue crab, *Callinectes sapidus* (Rathbun), predation in Chesapeake Bay. *J. Exp. Mar. Biol. Ecol.*, 65, 67–81.

Boulding, E.G. (1984). Crab-resistant features of burrowing bivalves: decreasing vulnerability by increasing handling time. *J. Exp. Mar. Biol. Ecol.*, 76, 201–223.

Bowmer, T. & Keegan, B.F. (1983). Field survey of the occurrence and significance of regeneration of *Amphiura filiformis* (Echinodermata: Ophiouridae) from Galway Bay, west coast of Ireland. *Mar. Biol.*, 74, 65–71.

Byers, J.E. (2002). Physical habitat attribute mediates biotic resistance to non-indigenous species invasion. *Oecologia*, 130, 146–156.

Byers, J.E. (2005). Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. *Ecology* 86(2), in press.

Coen, L.D. & Heck, K.L. (1991). The interacting effects of siphon nipping and habitat on bivalve (*Mercenaria-mercenaria*(L)) growth in a subtropical seagrass (*Halodule-wrightii aschers*) meadow. *J. Exp. Mar. Biol. Ecol.*, 145, 1–13.

Dial, B.E. & Fitzpatrick, L.C. (1984). Predator escape success in tailed verses tailless *Scincella lateralis* (Sauria: Scincidae). *Anim. Behav.*, 32, 301–302.

Emmett, R.L., Nelson, S.A., Stone, S.L. & Monaco, M.E. (1991). *Distribution and Abundance of Fish and Invertebrates in West Coast Estuaries Volume II: Species Life History Summaries*. ELMR Report No. 8. NOAA/NOS Strategic Environmental Assessment Division, Rockville, MD, p. 329.

de Goeij, P., Luttikhuizen, P.C., van der Meer, J. & Piersma, T. (2001). Facilitation on an intertidal mudflat: the effect of siphon nipping by flatfish on the burying depth of the bivalve *Macoma balthica*. *Oecologia*, 126, 500–506.

Haddon, M., Wear, R.G. & Packer, H.A. (1987). Depth and density of burial by the bivalve *Paphies vernticosa* as refuges from predation by the crab *Ovalipes catharus*. *Mar. Biol.*, 94, 25–30.

Haderlie, E.C. & Abbott, D.P. (1980). Bivalvia: the clams and allies. In: *Intertidal Invertebrates of California* (eds Morris, R.H., Abbott, D.P. & Haderlie, E.C.). Stanford University Press, Stanford, CA, pp. 355–411.

Hodgson, A.N. (1982). Studies on wound healing, and an estimation on the rate of regeneration, on the siphon of *Scrobicularia plana* (Da Costa). *J. Exp. Mar. Biol. Ecol.*, 62, 117–128.

Huang, C. & Sih, A. (1991). Experimental studies on direct and indirect interactions in a three trophic-level stream system. *Oecologia*, 85, 530–536.

Irlandi, E.A. & Mehlich, M.E. (1996). The effect of tissue cropping and disturbance by browsing fishes on growth of two species of suspension-feeding bivalves. *J. Exp. Mar. Biol. Ecol.*, 197, 279–293.

Kamermans, P. & Huitema, H.J. (1994). Shrimp (*Crangon-crangon* L.) browsing upon siphon tips inhibits feeding and growth in the bivalve *Macoma-balthica* (L). *J. Exp. Mar. Biol. Ecol.*, 175, 59–75.

Kerfoot, W.C. & Sih, A. (1987). *Predation: Direct and Indirect Impacts on Aquatic Communities*. University Press of New England, Hanover and London.

Korpimäki, E., Koivunen, V. & Hakkarainen, H. (1996). Microhabitat use and behavior of voles under weasel and raptor risk: predator facilitation? Behav. *Ecol.*, 7, 30–34.

Kotler, B.P., Brown, J.S., Slotow, R.H., Goodfriend, W.L., Strauss, M. (1993). The influence of snakes on the foraging behavior of gerbils. *Oikos*, 67, 309–316.

Lindsay, S.M. & Woodin, S.A. (1992). The effect of palp loss on feeding behavior of two spionid polychaetes: changes in exposure. *Biol. Bull.*, 183, 440–447.

Lindsay, S.M., Wethey, D.S. & Woodin, S.A. (1996). Modelling interactions of browsing predation, infaunal activity, and recruitment in marine soft-sediment habitats. *Am. Nat.*, 148, 684–699.

Losey, J.E. & Denno, R.F. (1998). Positive predator-predator interactions: enhanced predation rates and synergistic suppression of aphid populations. *Ecology*, 79, 2143–2152.

Miller, B.S. (1967). Stomach contents of adult starry flounder and sand sole in East Sound, Orcas Island, Washington. *J. Fish. Res. Board. Can.*, 24, 2515–2526.

Mouritsen, K.N. (2004). Intertidal facilitation and indirect effects: causes and consequences of crawling in the New Zealand cockle. *Mar. Ecol. Prog. Ser.*, 271, 207–220.

Peterson, C.H. & Quammen, M.L. (1982). Siphon nipping: its importance to small fishes and its impact on growth of the bivalve *Protothaca staminea* (Conrad). *J. Exp. Mar. Biol. Ecol.*, 63, 249–268.

Rosenheim, J.A., Wilhoit, L.R. & Armer, C.A. (1993). Influence of intraguild predation among generalist insect predators on the suppression of an herbivore population. *Oecologia*, 96, 439–449.

Sasaki, K., Kudo, M., Tomiyama, T., Ito, K. & Omori, M. (2002). Predation pressure on the siphons of the bivalve *Nuttallia olivacea* by the juvenile stone flounder *Platichthys bicoloratus* in the Natori River estuary, north-eastern Japan. *Fish. Sci.*, 68, 104–116.

Seitz, R.D., Lipcius, R.N., Hines, A.H. & Eggleston, D.B. (2001). Density-dependent predation, habitat variation, and the persistence of marine bivalve prey. *Ecology*, 82, 2435–2451.

Seitz, R.D., Marshall, L.S. Jr, Hines, A.H. & Clark, K.L. (2003). Effects of hypoxia on predator-prey dynamics of the blue crab *Callinectes sapidus* and the Baltic clam *Macoma balthica* in Chesapeake Bay. *Mar. Ecol. Prog. Ser.*, 257, 179–188.

Sih, A., Englund, G. & Wooster, D. (1998). Emergent impacts of predators on prey. *TREE*, 13, 350–355.

Skilleter, G.A. & Peterson, C.H. (1994). Control of foraging behavior of individuals within an ecosystem context: the clam *Macoma balthica* and interactions between competition and siphon cropping. *Oecologia*, 100, 268–278.

Smith, T.E., Ydenberg, R.C. & Elner, R.W. (1999). Foraging behaviour of an excavating predator, the red rock crab (*Cancer productus* Randall) on soft-shell clam (*Mya arenaria* L.). *J. Exp. Mar. Biol. Ecol.*, 238, 185–197.

Soluk, D.A. (1993). Multiple predator effects: predicting combined functional response of stream fish and invertebrate predators. *Ecology*, 74, 219–225.

Tallqvist, M. (2001). Burrowing behavior of the Baltic clam *Macoma balthica*: effects of sediment type, hypoxia and predator presence. *Mar. Ecol. Prog. Ser.*, 212, 183–191.

Taylor, G.M. (2000). Maximum force production: why are crabs so strong? Proc. *R. Soc. Lond. B*, 267, 1475–1480.

Virnstein, R.W. (1977). The importance of predation by crabs and fishes on benthic infauna in Chesapeake Bay. *Ecology*, 58, 1199–1217.

de Vlas, J. (1979). Secondary production by siphon regeneration in a tidal flat population of *Macoma balthica*. *Neth. J. Sea. Res.*, 19, 147–164.

Whitlow, W.L., Rice, N.A. & Sweeney, C. (2003). Native species vulnerability to introduced predators: testing an inducible defense and a refuge from predation. *Biol. Inv.*, 5, 23–31.

Zaklan, S.D. & Ydenberg, R. (1997). The body size-burial depth relationship in the infaunal clam *Mya arenaria*. *J. Exp. Mar. Biol. Ecol.*, 215, 1–17.

Zar, J.H. (1996). *Biostatistical Analysis*, 3rd edn. Prentice Hall, Upper Saddle River, NJ.

Zwarts, L. (1986). Burying depth of the benthic bivalve *Scrobularia plana* (Da Costa) in relation to siphon-cropping. *J. Exp. Mar. Biol. Ecol.*, 101, 25–39.

Zwarts, L. & Wanink, J. (1989). Siphon size and burying depth in deposit and suspension-feeding benthic bivalves. *Mar. Biol.*, 100, 227–240.

Zwarts, L., Blomert, A.M., Spaak, P. & de Vries, B. (1994). Feeding radius, burying depth and siphon size of *Macoma balthica* and *Scrobularia plana*. *J. Exp. Mar. Biol. Ecol.*, 183, 193–212.

Editor, Gary Belovsky
Manuscript received 25 August 2004
First decision made 4 October 2004
Manuscript accepted 21 October 2004