

## SYMBIOSIS BETWEEN AN ALPHEID SHRIMP AND A XANTHOID CRAB IN SALT MARSHES OF MID-ATLANTIC STATES, U.S.A.

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### A B S T R A C T

Instances of mutualism and commensalism between alpheid shrimp and other marine invertebrates and fish are common in tropical waters. In this study, we present evidence that the temperate alpheid big-clawed snapping shrimp (*Alpheus heterochaelis*) participates in a symbiosis with the black-clawed mud crab (*Panopeus herbstii*), which constructs and maintains burrows in salt marshes of mid-Atlantic states, U.S.A. We surveyed eight mid-Atlantic salt marshes and found that 11% of occupied crab burrows ( $n = 1042$ ) also housed *Alpheus*. Feeding trials showed that whereas *Panopeus* readily consumes other marsh Crustacea (i.e., grass shrimp and fiddler crabs), it will not prey on snapping shrimp. *Alpheus* caged in the marsh without access to mud crab lairs could not construct burrows. These results suggest that alpheid shrimps, thought to be limited in distribution to unvegetated mudflats and oyster reefs, may expand their intertidal range by living commensally with *Panopeus herbstii* in salt marsh habitats.

Tropical marine communities are characterized by mutualistic and commensal relationships typical of alpheid shrimp (Levinton, 1982; Nybakken, 1982). For example, in shallow-water Caribbean environments, the red snapping shrimp, *Alpheus armatus* (Rathbun) lives in a mutualistic relationship with the ringed anemone, *Bartholomea annulata* (Leseur), where the shrimp ward off potential predators with powerful snaps and the cnidarian hosts provide shelter from intense fish predation beneath stinging tentacles (Smith, 1977). Similarly, *Alpheus lottini* (Guérin-Méneville) guards the coral *Pocillopora damicornis* (Linnaeus) against seastar predation by snipping off tube feet of encroaching echinoderms and, in exchange, receives nutritional benefits by feeding on coral mucus (Patton, 1974; Glynn, 1976). Snapping shrimp have also been shown to live mutualistically with goby fish in burrows. In this interaction, gobies act as lookouts for potential predators while alpheid shrimp provide shelter by excavating burrows (Kaplus, 1987). Although numerous symbioses involving snapping shrimp have been described in tropical waters with important

ecological and evolutionary consequences (Levinton, 1982; Nybakken, 1982; Duffy, 1996), relatively few have been suggested in temperate systems.

Along the U.S. mid-Atlantic seaboard, the bigclaw snapping shrimp, *Alpheus heterochaelis* (Say), is associated with intertidal and shallow subtidal soft-sediment habitats (e.g., oyster reefs and mudflats) and is reported to be restricted to shallow burrows and depressions beneath oyster shells adjacent to salt marsh habitat (Hay and Shore, 1915; Williams, 1965; Nolan and Salmon, 1970; Lippson and Lippson, 1984; Williams, 1984). These shrimp are relatively sedentary, filter feeding from within their shelter from waters drawn into burrows by paddling with modified pleopods (Nolan and Salmon, 1970; Lippson and Lippson, 1984). Their large chelae allow them to manipulate debris to construct living spaces within the matrix of oyster shells, but their “spindly” hind appendages and small size (to 50 mm) likely restrict their burrowing activities to soft mud habitats (Williams, 1984). Other species able to penetrate thick root matrix or marsh grass and

establish burrows, however, may provide snapping shrimps with opportunity to extend range into adjacent salt marshes through symbiosis.

In mid-Atlantic salt marshes, the blackclaw crab, *Panopeus herbstii* (H. Milne Edwards), is widely distributed and locally abundant (Silliman and Zieman, 2001; Silliman *et al.* unpublished). Large mud crabs (35–55 mm carapace width) construct U-shaped burrows in the marsh root mat and are ambush predators on common marsh mollusks (e.g., marsh periwinkle, *Littoraria irrorata*, and mud snail, *Illyanassa obsoleta*). *Panopeus* burrows are typically 5–10 cm in depth, with two openings and a shelled joist (either ribbed mussels or oysters). During low tide, burrows commonly remain filled with water, acting as small intertidal pools on the marsh surface. While excavating *Panopeus* burrows in a Virginia salt marsh (Silliman and Zieman, 2001), we observed *Alpheus heterochaelis* living in a number of crab-occupied burrows. In this study, we examine the generality of this observation and begin to test whether there is a positive relationship between *Panopeus* and *Alpheus* in the temperate western Atlantic, as has been observed between xanthoid crabs and alpheid shrimps in the tropical reef Indo-West Pacific (Lassig, 1977; Vannini, 1985).

#### MATERIALS AND METHODS

We surveyed mud crab lairs for presence of snapping shrimps in eight marshes along the mid-Atlantic seaboard in the summer of 1998 (North Carolina: Atlantic Beach and Ocracoke Island; Virginia: Hog Island, Cobb Island, Raccoon Island, and Parramore Sound marshes; Maryland: Assateague Island; Delaware: Bethany Spit). All sites were exposed to full strength sea water (29–34 ppt) and comprised back-barrier island, lagoon, and mainland marshes. Within each marsh, we randomly placed thirty 1-m<sup>2</sup> quadrats in low areas dominated by salt marsh cordgrass (*Spartina alterniflora* Loisel) and documented occupancy of lairs by mud crabs and snapping shrimps by: (1) using a stick probe inserted behind the burrow to coax crabs to the surface, and (2) disassembling lairs to look for snapping shrimp. Any mud clumps or shell clusters removed from crab burrows were carefully rinsed with sea water and examined for shrimp presence.

To examine whether or not *Panopeus* will consume *Alpheus* and other marsh crustaceans, we conducted no-choice predation experiments in the laboratory. We starved mud crabs ( $n = 20$  for each run, all ~40 mm in carapace width) for 48 hours, then presented each with one potential prey item. Organisms included in trials were abundant crustacean prey items in mid-Atlantic marshes (Daiber, 1982). Each crab and prey item were housed in a 500-mL plastic container with recirculating sea water to a depth of 2 cm. This level approximated water depth on the marsh surface when crabs are most actively feeding (i.e., just after

and before flood tide—Teal, 1962; Silliman *et al.*, unpublished).

We also caged snapping shrimp ( $n = 12$ ) on the marsh surface for four days to test whether *Alpheus* could excavate burrows in dense marsh root mat. On 10 × 10 cm areas of marsh substrate devoid of crab burrows in the intermediate height-form *Spartina* zone, we enclosed one adult *Alpheus* in each of 12 10 × 10-cm, 20-cm high, galvanized mesh enclosures (1-mm mesh). We monitored shrimp burrowing activity for four days.

#### RESULTS AND DISCUSSION

Our extensive survey of salt marshes across four mid-Atlantic states showed that *Alpheus heterochaelis* was present in 10.7% of crab-occupied burrows (112 of 1042 examined—12% occupancy in North Carolina and Virginia, 8% in Maryland, 6% in Delaware) and that density of snapping shrimp in *Spartina* low marsh habitats is ~1 shrimp/2 m<sup>2</sup> (= *Panopeus* lair density [~2.5 burrows/m<sup>2</sup>—Silliman *et al.*, unpublished] · shrimp occupancy rate [11%]). These findings: (1) suggest the symbiotic relationship between *Alpheus* and *Panopeus herbstii* initially observed in Virginia marshes is widespread in East Coast marshes; (2) expands current notions of *Alpheus* habitat associations to include marshes dominated by *Spartina alterniflora* in addition to previously documented areas of oyster reefs/shell debris and mud flats (Hay and Shore, 1915; Williams, 1965; Nolan and Salmon, 1970 Lippson and Lippson, 1984; Williams, 1984); and (3) expands the known northern limit of *Alpheus heterochaelis* from the mouth of the Chesapeake Bay, Virginia, to Bethany Bay Spit, Delaware (Gosner, 1978). Excavation of lairs unoccupied by mud crabs ( $n = 257$ ) produced a strikingly different pattern, as snapping shrimp were never found in abandoned burrows. This suggests that snapping shrimp may associate with *Panopeus* for benefits other than those gained from inhabiting lairs alone (e.g., structural protection from large predators and/or desiccation stress). Potential associational benefits gained from cohabitation with crabs may include (1) lair maintenance by *Panopeus*, as unattended crab burrows in marshes quickly (i.e., ~5 days) collapse, fill in, or are taken over by roots and rhizomes (Bertness, 1984); (2) active protection from marsh predators (e.g., small blue crabs) that can enter burrows not occupied by *Panopeus* and consume *Alpheus*; and (3) access to food (e.g., snail tissues) left over from *Panopeus* predation events.

When living symbiotically with corals, alpheid shrimps ward off potential predators with thunderous snaps of their enlarged chelae

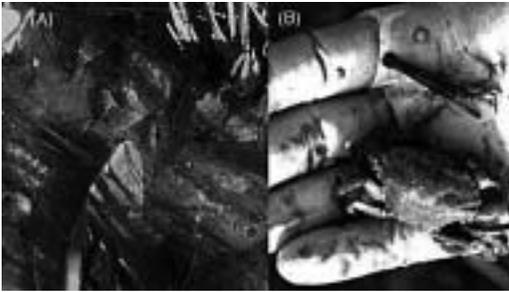


Fig. 1. (A) *Panopeus herbstii* in the salt marsh lying and waiting just outside the entrance of its U-shaped burrow to capture periwinkle snails. There is about 10 cm of water on the marsh surface. Periwinkle middens are visible next to entrance of mud crab lair. (B) Picture of same mud crab after lair was excavated and the *Alpheus heterochaelis* living symbiotically in its lair was found.

(Glynn, 1976). During excavation and disturbance of crab lairs (Fig. 1), we often heard the loud snap of *Alpheus heterochaelis*. In the observed *Panopeus*-shrimp symbiosis (Fig. 1), snapping shrimp may similarly ward off predators (e.g., blue crabs, fish) with their snaps and also indirectly alert mud crabs to predation threats. Potential for cooperative guarding of lairs is suggested by mutualistic associations in tropical reef systems in which alpheid shrimps and xanthoid crabs co-defend shared habitats (Lassig, 1977; Vannini, 1985). Common enemies are driven from shelters by aggressive attacks by crabs and snapping by shrimp. Mud crabs would benefit from shrimp presence if snapping alerted the crab to move deep into its burrow to decrease chance of predation, a benefit most important during flood tides when natant predators (e.g., red drum) enter the marsh to forage (Boothby and Avault, 1971).

Laboratory feeding experiments provided further evidence for symbiosis between *Panopeus* and the bigclaw snapping shrimp. In all twenty feeding trials, starved adult *Panopeus* did not consume *Alpheus* (Table 1). This pattern occurred even though *Panopeus* readily consumed small conspecifics, fiddler crabs, and grass shrimp similar in size to *Alpheus* (Table 1). During feeding trials, we observed *Alpheus* crawling over, on top of, and under mud crabs (~2 hours) without any apparent repercussions from *Panopeus*, suggesting that living symbiotically may be a common occurrence and that mud crabs recognize *Alpheus* as a commensal rather than potential prey. This last suggestion is supported by evidence of host recognition of

Table 1. Potential crustacean prey of *Panopeus herbstii* in mid-Atlantic marshes. Crabs ( $n = 20$  for each run) were starved for 48 hours and then presented with one prey item in no-choice predator experiments. The number of crabs that consumed the prey item is given in parenthesis.

Potential food items	Consumed
Mud fiddler ( <i>Uca pugnax</i> )	18
Sand fiddler ( <i>Uca pugilator</i> )	15
Snapping shrimp ( <i>Alpheus heterochaelis</i> )	0
Small (< 10 mm) mud crab ( <i>Panopeus herbstii</i> )	15
Grass shrimp ( <i>Palaemonetes pugio</i> )	14

symbiotic snapping shrimp in other mutualistic relationships (Karplus, 1981; Vannini, 1985). Furthermore, *Panopeus* may tolerate/seek direct contact by *Alpheus* if the latter acts as a cleaner similar to tropical alpheids with xanthoid crabs (Lassig, 1977; Vannini, 1985) and gobiid fish (Karplus *et al.*, 1974). When placed in small containers with other large marsh crabs, *Alpheus* did not display intimate behavior (purple marsh crab, *Sesarma reticulatum* (Say), and small blue crabs, *Callinectes sapidus* Rathbun; 3–5 cm carapace width;  $n = 10$  for each). Instead, they actively avoided contact (i.e., they moved to opposite ends of the plastic container) and, in eight of ten cases, large blue crabs (carapace width >14 cm) consumed *Alpheus*, suggesting there is no chemical deterrent preventing *Panopeus* from consuming snapping shrimp.

Snapping shrimp caged on the marsh surface showed no capability of excavating burrows in the marsh matrix. After four days, there was no burrow formation nor any visible signs of attempts to construct a burrow (i.e., small depressions in the marsh). This suggests *Alpheus* is reliant on mud crabs for burrow generation in marsh habitat and is consistent with other studies suggesting that burrowing by snapping shrimp is limited to areas with soft sediments and available shell debris (Hay and Shore, 1915; Williams, 1965; Nolan and Salmon, 1970; Lippson and Lippson, 1984; Williams, 1984). The possibility that *Alpheus* relies on *Panopeus* for lair construction is consistent with a recent review by Boltana and Thiel (2001) which showed that most symbiotic species of alpheid shrimps in tropical waters inhabit burrows constructed and maintained by other species. Six of twelve individuals in our caging experiment died after four days (most likely from desiccation stress, as carapaces were noticeably collapsed). This suggests *Alpheus* is obligately dependent on mud crab burrows for survival in marsh habitat.

Together, our large-scale marsh survey and experimental results show that *Panopeus herbstii* and *Alpheus heterochaelis* commonly live symbiotically in East Coast salt marshes and that there may be an obligate, commensal relationship, with snapping shrimp being reliant on mud crabs for generation and maintenance of subsurface shelter in root-dominated marsh matrix. Our observations of *Alpheus heterochaelis* snapping during burrow excavation suggest *Panopeus* may receive indirect benefits from this interaction as well (i.e., an early warning system—as shrimp snap to avoid predation, mud crabs may be alerted to predator presence). Further experiments are needed to elucidate degree, directionally, and specific benefit of potential positive interactions in this relationship. This study provides evidence that alpheid-shrimp symbioses, common in tropical systems, also occur in the temperate marine environments of the western Atlantic.

#### ACKNOWLEDGEMENTS

Our work was supported by the Virginia Coast Reserve—Long Term Ecological Research project, the Nature Conservancy, and the Odum Foundation. We thank three anonymous reviewers whose comments improved this manuscript.

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RECEIVED: 11 March 2003.

ACCEPTED: 18 June 2003.