Hydrobiologia **365**: 233–239, 1998.
J. L. Norenburg & P. Roe (eds), Fourth International Conference on Nemertean Biology.
©1998 *Kluwer Academic Publishers. Printed in Belgium.*

Nemertean predation on the tropical fiddler crab *Uca musica*

John H. Christy[1], Seiji Goshima[2], Patricia R. Y. Backwell[1] & Thomas J. Kreuter[1]
[1] *Smithsonian Tropical Research Institute, Apartado 2072, Balboa, Ancon, Republic of Panama*
[2] *Department of Biology and Aquaculture, Faculty of Fisheries, Hokkaido University, Hakodate 041, Japan*
(For correspondence from the U.S.: Smithsonian Tropical Research Institute, J. H. Christy, Unit 0948, APO AA 34002-0948, U.S.A)

Key words: Hoplonemertean, fiddler crab, predatory behavior, anti-predator defenses, intertidal, Panama

Abstract

We saw 79 predatory interactions between a new species of monostiliferous, suctorial hoplonemertean and the fiddler crabs *Uca musica* (77 cases) and *U. stenodactylus* (2 cases). At an intertidal sand bar in the Pacific entrance of the Panama Canal, worms ate about 0.1% of the adult crab population per day. The mode of attack and the spatial and temporal distributions of interactions suggest the worm is an ambush predator. When struck by a worm's sticky, mucous-covered proboscis, crabs produced copious foam from their buccal area. Mucous-laden crabs that escaped, again foamed indicating that the foam may counteract the mucus. If the attack led to a kill, the struggling crab soon became quiescent, as is typical in other nemertean-prey interactions. The worm inverted its proboscis, found ingress to the crab's body and fed. Crabs escaped by autotomizing appendages entwined by the proboscis, by forcefully pulling away and by remaining quiescent, then moving away when the worm inverted its proboscis and before it entered the crab. Immobility, a response to visual predators, may falsely indicate paralysis to the worm and cause it to invert its proboscis, thereby providing the crab with an opportunity to escape. This predator-prey interaction seems to incorporate generalized predator tactics and fortuitous prey defenses that give worms and crabs about an even chance of success.

Introduction

The prey of less than ten percent of the approximately 260 species of suctorial hoplonemerteans have been described (McDermott & Roe, 1985). Free-living marine species typically specialize on amphipods or isopods (e.g. McDermott, 1984; Roe, 1993). The ecology and behavior of specialist nemertean predators and their prey are known from relatively few field studies (e.g., Roe, 1993; Thiel & Reise, 1993).

We have discovered a new species (*fide* J. Norenburg) of monostiliferous, suctorial, intertidal hoplonemertean that eats fiddler crabs, a previously unreported nemertean prey. Voucher specimens of the nemertean are deposited at the Smithsonian National Museum of Natural History (USNM# 169968–169971). Here we describe the ecological setting, the distribution of predatory interactions in space and time, the predatory behavior of the worm and the escape behavior of the crab. We tentatively conclude that neither worm nor crab exhibit special traits that have evolved in response to each other as predator and prey.

Natural history and behavior of *Uca musica*

As this is the first report of nemertean predation on fiddler crabs, we will briefly summarize features of the natural history and behavior of *Uca musica* Rathbun that pertain to this interaction. We base our summary on Crane (1975), Zucker (1976, 1978, 1981) and our own observations.

U. musica (1 cm adult carapace width) digs burrows 10–30 cm deep in mid to high intertidal sand substrates in estuaries and bays on tropical Eastern-Pacific shores. Crabs are active on the surface when their habitat is

exposed to the air during the day. Few crabs emerge on days with low tides before 0700 h and after 1700 h, and when neap high tides are too low to flood their habitat. As is typical of intertidal crabs (Morgan & Christy, 1995), at the population level *U. musica* has a biweekly reproductive rhythm.

Crabs emerge from their plugged burrows about 2–2.5 h before low tide, after their habitat has fully drained. About 6 h later, they again plug their burrows and stay below. During the first 1–2 h of the activity cycle, crabs feed intensively on the surface near their burrows by scraping up bits of sediment with their small chelae. At about the time of low tide, crabs begin to move between burrows: sexually receptive females sequentially visit several courting males before they choose a mate, reproductively active males fight for burrows and some non-breeding crabs seek a new burrow and feeding site. By the end of the activity period, crabs usually will have fed upon or walked over nearly every cm^2 in their habitat.

Study site

We observed worms and crabs at an intertidal sand bar on the west bank of the Pacific entrance of the Panama Canal, about 1 km upstream of the Bridge of the Americas. The bar extends 125 m from a sparsely wooded (white mangrove, *Laguncularia racemosa*) intertidal sand island at its eastern higher end, westward and down toward the shore. The bar caps a layer of mangrove peat mixed with basalt and quartz stones. The well-drained sand layer grades from over 1 m deep at the shifting crest of the bar to a few cm on the lower bank.

U. musica lives on the upper well-drained banks of the bar and is most abundant (12–15 adults m^{-2}) in an approximately 265 m^2 area on the north facing bank adjacent to the island. The tide may not cover this area for up to 4 d during a given month. *Uca stenodactylus* (Milne-Edwards & Lucas) lives just below the lower intertidal range of *U. musica*.

Methods

From 13 February to 10 May, one to three persons were at the site for 5–6 h (1–2 h before to 3–4 h after low tide) during every daytime low tide. On days with dawn and dusk low tides, we visited the site twice. On 14 February, one of us (TJK) first saw a worm attack a male *U. musica*. Until the end of April, while conducting other studies, we made fortuitous observations on worm-crab interactions.

On ten days during the period 27 April to 8 May, we watched systematically for nemertean predation for a minimum of 20 minutes each hour we were at the site. We located attacks by the contrast between the bright red-orange nemertean proboscis and the sand background. We noted the time of attack and we sometimes timed phases of the interaction. We observed attacks closely, documented them on film and wrote a narrative of each. We marked with numbered plastic sticks and later mapped the locations of attacks, including those that lead to escapes, and the exoskeletons of crabs that were eaten by the worm. We collected and preserved (70% ethanol) these exoskeletons and later measured (carapace width) and examined them under a microscope. On 4–6 April we marked with un-numbered sticks the locations of 13 kills. We included these in the analysis of the spatial distribution of predation.

Results

Frequency of interactions

We observed or saw evidence of 79 predatory interactions between nemerteans, *U. musica* (77 cases) and *U. stenodactylus* (2 cases). We saw only 2 predation events outside the 265 m^2 area where *U. musica* was most abundant. During the 10-day period, worms killed 33 crabs (2–9 d^{-1}). Based on visual counts of the density of courting males, and assuming an even sex ratio, we estimate that 3 000 to 4 000 adult crabs lived in the 265 m^2 area. Hence, nemerteans ate about 0.1% of these crabs d^{-1}. We recorded the maximum of 11 kills on 16 March when low tide occurred at 0928 h and crabs resumed full surface activity after having spent four days underground because the tides were too low to cover their habitat.

Spatial distribution and timing of interactions

We marked the location of 56 predatory interactions but lost 15 markers before we could map them. We assume these losses were random with respect to location. Worms attacked crabs throughout the area but less often at the edges of the crab distribution, especially in the higher, drier area (Figure 1a, b). Five pairs of markers were unusually close together (0, 8, 9, 11, 12 cm), about 1/10 of the average distance separat-

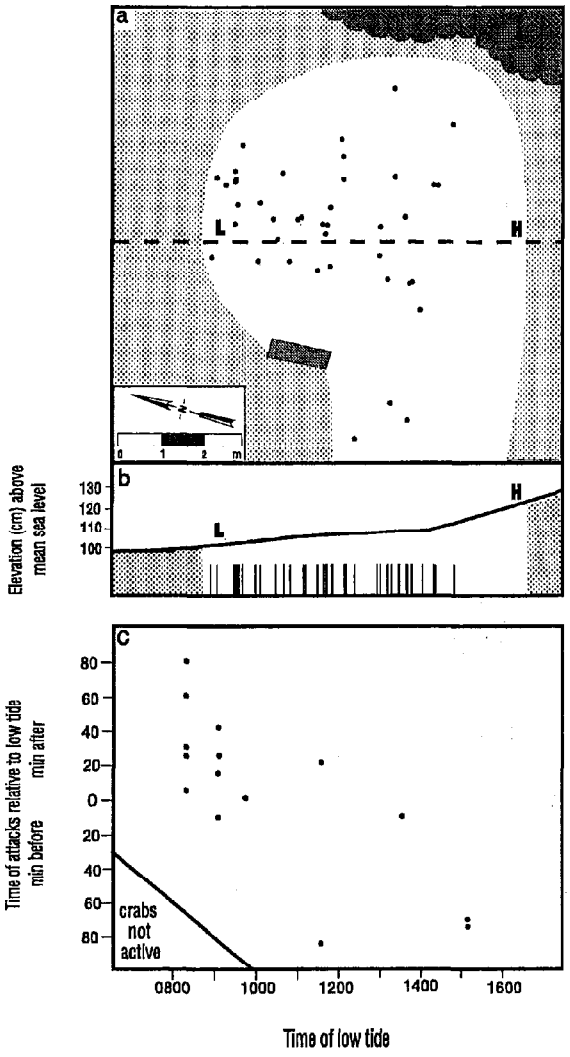

Figure 1. The spatial and temporal distributions of predatory interactions between nemerteans and *U. musica*. a: Locations of 41 interactions in the area of greatest crab density. Shading shows the mangrove canopy, an observation platform and the limits of *U. musica* burrows. b: Locations of interactions on the elevation gradient from the lower (L) to the higher (H) limit of crab burrows. c: Attack times relative to the times of low tide on six days. The diagonal line shows the approximate time of crab emergence.

ing other nearest-neighbor marker pairs (see below). Four pairs were placed during the 10 day period of systematic observation. Two of these pairs showed the locations of kills made 2 and 3 d apart. The other two pairs marked kills followed by escapes 2 and 10 d later. If one worm made both attacks in each of these pairs, as suggested by their unusually close spacing, then worms may attack as often as every other day.

We used the Clark & Evans (1954) nearest-neighbor method to analyze the 'within-clump' dispersion of predatory interactions. We reduced edge effects by excluding three isolated events to the west (Figure 1a). We then delimited a polygonal area by drawing straight lines between six markers at the edges of the distribution. These markers could be nearest-neighbors of more central ones (one case) but were otherwise not included in the analysis. Finally, we assumed (see above) that markers in each of the five unusually close pairs showed the activities of one worm. Hence, we treated the five close pairs as one point each, positioned mid-way between the markers.

Twenty-seven interactions with a mean separation of 97 cm were within the 77.9 m^2 polygonal area. The spatial pattern of interactions was not different from random ($R = 1.143$, $p > 0.30$).

We recorded the time of 15 attacks from the moment the worm struck the crab. Worms attacked from about 1.5 h before to 1.5 h after low tide and they attacked earlier relative to the time of low tide as low tide occurred later in the day (Figure 1c; $r = -0.78$, $p < 0.001$).

Predatory and feeding behavior

We saw 20 interactions from the beginning of an attack. Worms and crabs had about an equal chance of success (9 kills, 11 escapes). Attacked crabs usually were at the end of feeding furrows. We saw one attack on a receptive female as she approached a courting male and one on a male as he moved between burrows. Interactions varied according to the exact and dynamic nature of contact between the worm and crab. The following is a composite description of a 'typical' kill sequence.

The worm attacked by everting its proboscis, which usually first touched the crab's legs or (if male) the enlarged cheliped (Figures 2.1–9). Eversion was rapid, taking perhaps < 0.5 s for several cm of proboscis to contact and begin to entwine the crab. The proboscis adhered tenaciously to and tethered the crab. It laid down much sticky mucus that bound some of the crab's legs (Figure 2.10). Immediately when struck, the crab produced bubbles that quickly enveloped the frontal and lateral surfaces of the crab and the worm in foam (Figures 2.1–9). The proboscis did not avoid or recoil from the foam. It continued to evert, flex and further entwine the crab, often encircling it at the base of the legs or over the carapace (Figures 2.1, 16, 26). Due to

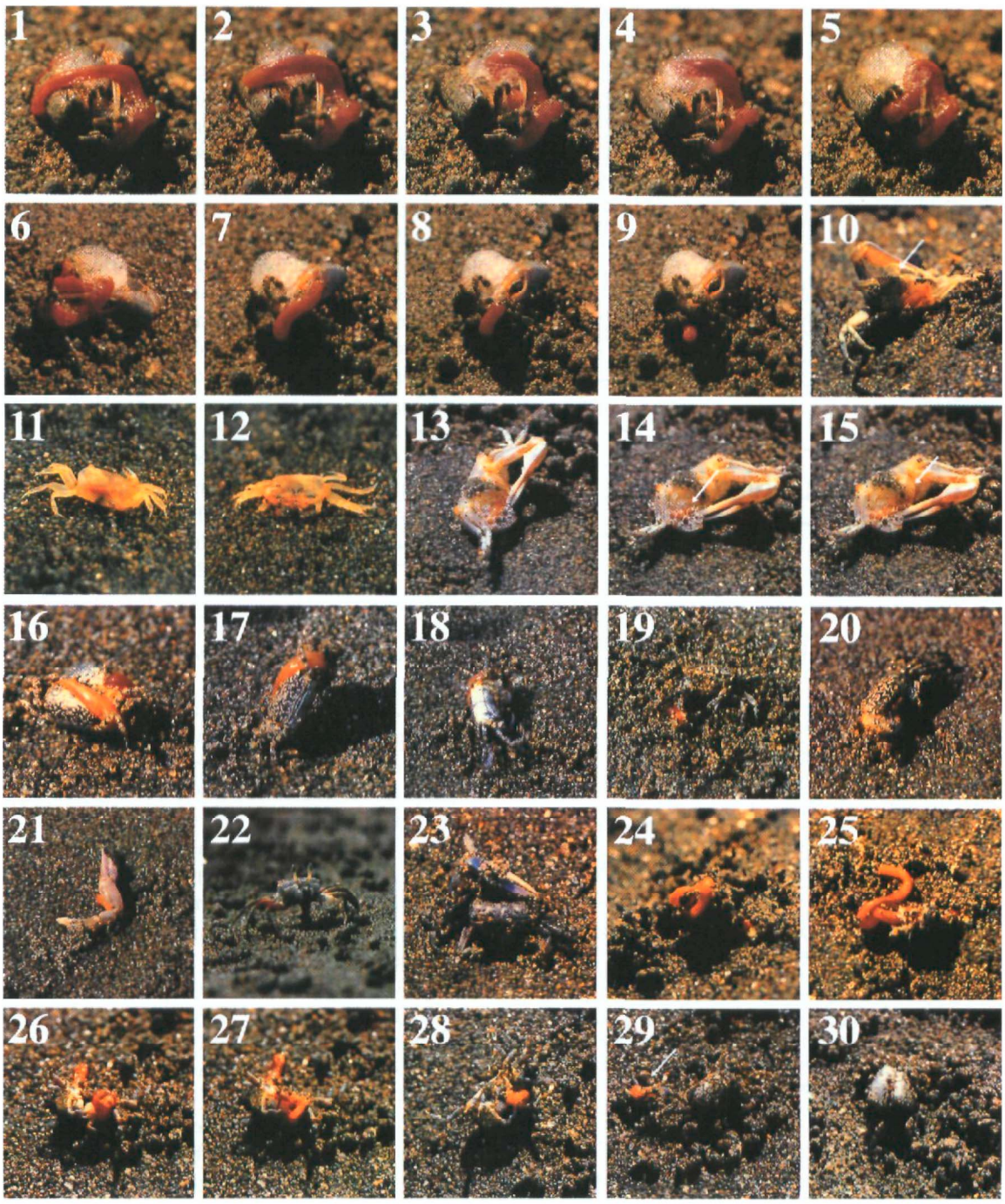

Figure 2. Predatory interactions between nemerteans and *U. musica* (except for 21, 22). *1–9*: The worm inverts its proboscis following presumed intoxication. *10*: A worm feeding. Note the mucous web between the crab's cheliped and carapace. *11, 12*: Late in the feeding process the worm is visible inside the crab. *13–15*: A worm moving between the sediment and crab in its mucous tube. *16–20*: An upside-down female struggles and escapes. *21, 22*: A male *U. stenodactylus* autotomized his cheliped and escaped. *23*: Autotomy does not always lead to escape. *24, 25*: A worm manipulating two autotomized legs. *26–30*: An upside-down female is quiescent, escapes by autotomizing two legs (arrow) when the worm withdraws, and then foams again as she cleans herself.

the action of the worm, the crab sometimes was turned over or tipped on one side (Figures 2.13–15, 17, 18).

The crab's appendages soon exhibited small amplitude twitches, then ceased all motion. We never saw the worm pierce the crab with its stylet. The worm inverted its proboscis (Figures 2.7–9; accurately timed cases: 3, 4, and 4.5 min after first eversion) and broke contact with the crab for several seconds. The anterior tip of the worm emerged, probed the crab, typically at the base of the legs and the edges of the buccal frame, and found a point of ingress (Figures 2.10, 12, 15). The crab discolored within minutes and was drained of tissue within an hour (35, 47 and 50 min) (Figures 2.11, 15). During the early feeding period we were unable to see into the crab. Later, when the carapace was translucent, we often saw the worm moving inside the crab's body (Figures 2.11, 12).

A mucous tube bridged the sediment and crab at the entry point. Worms rapidly retreated within this tube to the sediment if we touched the crab but they soon returned and resumed feeding (Figures 2.13–15). Great-tailed grackles (*Quiscalus mexicanus*) frequently eat *U. musica*. We saw a male grackle masticate and spit out a crab that had been eaten by a nemertean and a female examine and pass-over one while the worm was still feeding.

There was no strong sex bias (23 males, 18 females) in crabs killed and consumed by the worm. We examined the remnants of 38 crabs that had been eaten by nemerteans. In carapace width they averaged 9.4 ± 0.99 (s.d.) mm for males and 9.8 ± 0.67 mm for females, sizes typical of fully adult crabs (Crane, 1975). Thirteen crabs had autotomized a leg (11 cases) or a cheliped (2 cases) which remained glued to the crab by mucus (Figure 2.23). Worms did not consume the tissue in autotomized appendages. Twenty-four exoskeletons had some pigmented tissue in the distal segments of the legs or in the eye stalks. Worms never ingested the contents of the crab's digestive tract.

Escape behavior

Crabs escaped in several ways. We twice saw crabs dash away from an everting proboscis and we once saw an everted proboscis with no obvious close potential prey.

Crabs fully engaged by a worm struggled surprisingly little, especially if they remained upright. As the proboscis changed position they only briefly attempted to pull away from, pinch, kick or stab the worm with their dactyls. However, in one case (Figures 2.26–30), a female, who had been turned over by the worm, remained almost motionless for several minutes. As the proboscis inverted and just before it entered the sediment, the female autotomized two legs and escaped. More often, up-side-down crabs struggled vigorously and sometimes escaped (Figures 2.16–20). In four other cases crabs autotomized legs or (if male) their large cheliped (Figures 2.21, 22) and escaped when only these appendages were entwined by the inverting proboscis. Worms manipulated autotomized appendages for several minutes and sometimes again everted the proboscis as if searching for the crab (Figures 2.24, 25). Eventually they returned to the sediment without consuming any tissue. Crabs escaped 1.5, 3, 3, 6 and 10 min after the initial strike.

Crabs that escaped often again foamed as they cleaned themselves of mucus (Figures 2.20, 30). They showed no evidence of intoxication. They soon resumed normal surface activity (Figures 2.22) and sometimes walked directly over where they had been attacked, even when bits of mucus marked the spot. Worms never attacked again from the same point on a given day.

Discussion

At our study site, nemertean predation on *U. musica* was visually obvious and about as frequent as avian predation. It is remarkable that it has not been reported previously as *U. musica* has been observed at nearby sites for over five decades (Crane, 1941, 1975; Zucker, 1976, 1978, 1981).

We will discuss nemertean predation on *U. musica* with respect to six stages: encounter, detection, identification, approach, subjugation and consumption (Endler, 1991). We speculate freely on possible predatory mechanisms of worms and defense mechanisms of crabs. These speculations should not be regarded as substantiated conclusions from this preliminary study. Rather, they are possibilities that may warrant further investigation.

This nemertean appears to be an ambush predator. In this predatory mode, the predator's choice of where to hunt and the prey's activity jointly determined predator-prey encounter rates. With two exceptions, attacks occurred where crabs were most abundant indicating that worms hunt where they will encounter crabs most often. Crabs became active and worms attacked significantly earlier relative to low tide as the time of low tide occurred later in the day, and most attacks

occurred during the first half of the activity period. Worms probably hunt from fixed positions established before crabs become active. If worms rose to the surface after crabs began to feed, they might come up where crabs have already fed and are less likely to pass again. Crabs usually were at the end of a feeding furrow when attacked, indicating that there may be a premium on striking the first time a crab passes.

Detection and identification seem biased in favor of the predator. Worms may detect crabs by touch or they may use their two anterior sub-terminal pigment spots, which presumably are photosensitive, to detect crabs by their shadow. We saw no patterns in crab movements that indicate crabs detect worms.

Approach and subjugation begin when a worm everts its proboscis. At the moment of attack, quickness seems equally important to predator and prey. Subjugation may depend on the production and spread of mucus by the worm and crab defenses against it. Apart from other possible functions (Crane, 1975, 472; Holmquist, 1989), we speculate that foam bathing may counter the effects of nemertean mucus. Feeding fiddler crabs periodically discharge on the sediment a brownish fluid from their buccal cavity. It may be a slurry of gastric juice and indigestible material ground by the gastric mill. The foam crabs produced when attacked often had a brown or yellow tinge suggesting the presence of this fluid. Diatoms, which produce abundant mucopolysaccharides (Darley, 1977), are a major component of fiddler crab diets (Montague, 1980; Wolcott & O'Connor, 1992). Enzymes that attack mucopolysaccharides probably are present in fiddler crab gastric fluids. Hence, crabs that discharge gastric fluids and disperse them with foam may thereby chemically attack the nemertean mucus. Crabs that escaped usually again foamed as they cleaned themselves of mucus, supporting a cleansing function for foaming, regardless of the exact mechanism.

Intoxication is the pivotal step in subjugation (McDermott & Roe, 1985). The appendages of attacked crabs sometimes 'shivered' just before the crab became quiescent, presumably an effect of the worms toxins. The crab's hard exoskeleton probably is its primary defense. Since intoxicated prey are immobile, worms may use prey quiescence as a cue to invert the proboscis and begin feeding. Hence, crabs that struggle little, but are not intoxicated, may cause worms to invert and increase their chance for escape.

We suggest that quiescence may be a fortuitous effect of a response selected by visual predators, not nemerteans. Except for courting males, who usually blanch to white, *U. musica* appear cryptic to humans due to the color pattern on their dorsal carapace and legs (Figures 2.19, 29). Crabs are uniformly light colored below (Figure 2.18) and visually conspicuous when upside-down. When threatened and unable to escape, *U. musica* become motionless. This presumably increases that chance that they will escape detection by visual predators. Nemerteans may elicit this freeze response, especially from crabs that keep upright.

Paralyzed crabs had no apparent defense against consumption. In one case a nemertean paralyzed a crab, inverted its proboscis and then searched for but did not relocate the crab. This crab did not recover.

From proboscis eversion through consumption, the behavior of this hoplonemertean and the behavior of species that specialize on amphipods and isopods are similar (McDermott, 1984; McDermott & Roe, 1985; Roe, 1993). The slight differences, e.g., movement of worms deep inside crabs, but not other crustacean prey, may be attributed to the unusually large size of fiddler crabs. The defenses of other prey have not been described in detail. Many of the defenses of *U. musica* may have evolved due to their use in other contexts and fortuitously serve as defenses against this predator.

This is the first report of nemertean predation of fiddler crabs, the largest known crustacean prey of a nemertean. Fiddler crabs seem unlikely prey for nemerteans as they are so responsive, agile and fast. However, ambush predation obviates search and pursuit by the worm, predatory phases in which crabs would have a clear advantage. Fiddler crabs are common on soft intertidal sediments throughout the tropics. They often occur at high densities and, during most low tide activity periods, they feed upon or walk over nearly the entire surface of the sediment in their habitat. It seems likely that nemerteans elsewhere have capitalized on these features of crab behavior by adopting an ambush mode of predation.

Acknowledgements

We thank Mary Rice for initial guidance, Jon Norenburg and Pamela Roe for their enthusiastic encouragement and the Smithsonian Tropical Research Institute and the Japanese Ministry of Education, Culture and Science for support.

References

Crane, J., 1941. Eastern Pacific expeditions of the New York Zoological Society. XXVI. Crabs of the genus *Uca* from the west coast of Central America. Zoologica, NY 26: 145–208.

Crane, J., 1975. Fiddler crabs of the world (Ocypodidae: genus *Uca*). Princeton University Press, Princeton (NJ), 736 pp.

Darley, W. M., 1977. Biochemical composition. In D. Werner (ed.), The Biology of Diatoms. Botanical Monographs 13, Blackwell Scientific Publications, Oxford: 198–223.

Endler, J., 1991. Interactions between predator and prey. In J. R. Krebs & N. B. Davies (eds), Behavioural Ecology and Evolutionary Approach, Blackwell Scientific Publications, Oxford: 169–196.

Holmquist, J. G., 1989. Grooming structure and function in some terrestrial Crustacea. In B. E. Felgenhauer, L. Watling & A. B. Thistle (eds), Functional Morphology of Feeding and Grooming in Crustacea, Crustacean Issues, 6. A. A. Balkema, Rotterdam: 95–114.

McDermott, J. J., 1984. The feeding biology of *Nipponnemertes pulcher* (Johnston) (Hoplonemertea), with some ecological implications. Ophelia 23: 1–21.

McDermott, J. J. & P. Roe, 1985. Food, feeding behavior and feeding ecology of nemerteans. Am. Zool. 25: 113–125.

Morgan, S. G. & J. H. Christy, 1995. Adaptive significance of the timing of larval release by crabs. Am. Nat. 145: 457–479.

Montague, C. L., 1980. A natural history of temperate western Atlantic fiddler crabs (genus *Uca*) with reference to their impact on the salt marsh. Contrib. mar. Sci. 23: 25–55.

Müller, W., 1989. Acoustical and vibrational communication and ecology of tropical and subtropical fiddler crabs. Zool. Jb. Syst. 116: 47–114.

Roe, P., 1993. Aspects of the biology of *Pantinonemertes californiensis*, a high intertidal nemertean. Hydrobiologia 266: 29–44.

Thiel, M. & K. Reise, 1993. Interaction of nemertines and their prey on tidal flats. Neth. J. Sea Res. 31: 163–172.

Wolcott, D. L. & N. J. O'Connor, 1992. Herbivory in crabs: Adaptations and ecological considerations. Am. Zool. 32: 370–381.

Zucker, N., 1976. Behavioral rhythms in the fiddler crab *Uca terpsichores*. In P. J. DeCoursey (ed.), Biological Rhythms in the Marine Environment. University of South Carolina Press, Columbia, SC: 145–159.

Zucker, N., 1978. Monthly reproductive cycles in three sympatric hood-building tropical fiddler crabs (genus *Uca*). Biol. Bull. 41: 281–286.

Zucker, N., 1981. The role of hood building in defining territories and limiting combat in fiddler crabs. Anim. Behav. 29: 387–395.