Journal of Experimental Marine Biology and Ecology 413 (2012) 177–183

Contents lists available at SciVerse ScienceDirect

Journal of Experimental Marine Biology and Ecology

journal homepage: www.elsevier.com/locate/jembe

Prey selection in crustacean-eating fishes following the invasion of the Asian shore crab *Hemigrapsus sanguineus* in a marine temperate community

Kari B. Heinonen *, Peter J. Auster

Department of Marine Sciences, University of Connecticut, 1080 Shennecossett Road, Groton, 06340, CT, USA

ARTICLE INFO

Article history:
Received 28 April 2011
Received in revised form 20 December 2011
Accepted 21 December 2011
Available online 20 January 2012

Keywords:
Hemigrapsus sanguineus
Invasive species
Predation
Fish
Crab
Prey preference

ABSTRACT

The Asian shore crab *Hemigrapsus sanguineus* invaded the coast of Long Island Sound approximately twenty years ago and has become hyper-abundant and the most common crab species throughout the intertidal region. The success of the species is hypothesized to be due to reduced predation pressure in the invaded region. Recent observations document the expansion of *H. sanguineus* into shallow subtidal habitats (i.e., up to 5 m depth and up to 180 crabs m^{-2} in some habitats) where it is more accessible to a diversity of crustacean-eating predators. The role that higher trophic level predators might play in controlling populations of invasive species has seldom been investigated in marine communities. Here we conducted a series of prey-preference experiments under laboratory conditions to determine whether crustacean-eating fishes prefer *H. sanguineus* rather than native crab species, and to provide insight into how predator size and habitat type influence prey preference. Small size-class predators exhibited a clear preference for *H. sanguineus* in paired offerings of the invader versus native crab species while paired offerings for large size-class fishes resulted in mixed findings. Small size class predators demonstrated no preference when prey were set in a range of sediment type treatments (i.e., sand, pebble, cobble), while paired offerings for large size class predators resulted in mixed findings. In general, the results from this study support our hypothesis that *H. sanguineus* is preyed upon preferentially by native crustacean-eating fishes but sediment type and predator size play an important role in determining that preference. Preference for the invasive crab over the native prey items in some settings suggests prey switching could occur in areas where the invader is abundant. We suggest that future field studies focus on the role that crustacean-eating fishes can play in biological control of invasive crab populations and how management of predators can influence the impact of invaders.

1. Introduction

Marine invasions are increasing on a global scale and have become an issue of critical importance because of their real and potential impact on marine ecosystems (Bax et al., 2001; Carlton, 1989, 1996; Carlton and Geller, 1993; Molnar et al., 2008; NIMPIS, 2009). Invasive species can act as vectors for new diseases, reduce biological productivity, degrade habitat structure, threaten fisheries, and alter food webs through ecological processes such as competition and predation (Carlton, 1999; Clarke et al., 1984; Mack et al., 2000; Vitousek et al., 1996). The resultant decline or elimination of native populations can have negative impacts on ecosystem function, patterns of diversity, coastal economies and public health (Lafferty and Kuris, 1996; Vitousek et al., 1997). However, specific direct and indirect effects of most invasive species remain unknown and poorly predicted (Kolar and Lodge, 2001; Ruiz et al., 1997). Understanding food web interactions are one of the few foundations for predicting impacts of invasions (Byrnes et al., 2007; Pinnegar et al., 2001; Zaret and Paine, 1973). Such impacts include the potential change in feeding patterns of native predators with the establishment of an invasive species that may serve as prey (Maerz et al., 2005; Rilov et al., 2002) and the resultant changes in food webs (Byrnes et al., 2007; Ruiz et al., 1997).

The Asian shore crab, *Hemigrapsus sanguineus*, invaded the coast of Long Island Sound (LIS) approximately twenty years ago (Williams and McDermott, 1990) and has become the most common crab species throughout the intertidal region with hyper-abundant population densities exceeding 100 crabs m^{-2} (Ahl and Moss, 1999; Gerard et al., 1999; Lohrer and Whitlach, 1997; K. Heinonen unpub. data). The ecological impacts of this invasion in the intertidal can be extreme. For example, experiments demonstrated that predation by *H. sanguineus* caused significant declines in blue mussel *Mytilus edulis* (Lohrer and Whitlach, 2002), green crab *Carcinus maenas* (Jensen et al., 2002), and macroalgae (Brousseau and Baglivo, 2005), all of ecological and economic importance. Recent observations document the expansion of *H. sanguineus* into shallow subtidal habitats (<1–5 m below mean low water with crab density up to180 m^{-2}; Gilman and Grace, 2009; K. Heinonen unpub. data), where it may

---

* Corresponding author. Tel.: +1 860 912 7791; fax: +1 860 405 9153.
E-mail addresses: kari.heinonen@uconn.edu (K.B. Heinonen), peter.auster@uconn.edu (P.J. Auster).

0022-0981/$ – see front matter © 2011 Elsevier B.V. All rights reserved.
doi:10.1016/j.jembe.2011.12.011

prey upon a wider range of native fauna and is more accessible to a wider variety of crustacean-eating predators. The ecological implications of this habitat expansion are poorly understood, and the interactions between crab predators and this potential prey species are virtually unknown.

Crab predators include crustacean-eating fishes or crabivores (sensu Garrison and Link, 2000), one of seven major classes of feeding guilds of fishes on the northeast United States continental shelf. The crabivore guild diet consists largely of crabs and other small decapod crustaceans. Along the coastal region of LIS, the principal species that comprise this guild are tautog *Tautoga onitis*, cunner *Tautogolabrus adspersus*, black sea bass *Centropristus striata*, and little skate *Leucoraja erinacea* (Collette and Klein-MacPhee, 2002; Gottschall et al., 2000). Results of recent studies and preliminary gut content analyses of a diversity of near-shore fishes collected from subtidal portions of eastern LIS (e.g. *T. onitis*, *T. adspersus*, striped bass *Morone saxatilis*, *C. striata*) demonstrate *H. sanguineus* is a prey item (Clark et al., 2006; K. Heinonen, unpub. data). Laboratory experiments conducted by Kim and O'Connor (2007) demonstrated that striped killifish (*Fundulus majalis*), a species common to marsh systems within LIS, readily consume *H. sanguineus* megalopae and 1st stage crabs. Additionally, examination of gut contents of *F. majalis* and the common mummichog *F. heteroclitus* collected from western LIS demonstrated that both species consume the crab, but that predation pressure was low (Brousseau et al., 2008). However, it remains unclear whether prey are consumed in proportion to their abundance in the environment or if predators selectively consume this invader. Understanding the details of such predator–prey interactions is necessary for assessing and predicting food web interactions between *H. sanguineus* and native fishes.

Selective foraging can have differential effects on prey abundance and distribution (Mascaro and Seed, 2000), and may influence invasion dynamics (Dudas et al., 2005). A fundamental aspect of understanding predator selectivity is the size relationship between the predator and the prey (Gill, 2003). The size of prey consumed generally increases with predator size in fishes. The range of prey sizes eaten also increases in larger predators, i.e. maximum prey size increases rapidly while minimum prey size may change only slightly over a large range of predator sizes (Hart and Reynolds, 2002). *H. sanguineus* attains a smaller average adult size (1.5–2.0 cm carapace width or cw, Kraemer et al., 2007) than many native crustacean species that serve as prey for fishes (e.g. mud crab *Panopeus herbstii* = 3.8 cm cw, green crab *Carcinus maenas* = 9 cm cw, or the carapace length of American lobster *Homarus americanus* = 8.3 cm; Weiss, 1995). Because of its relatively small size throughout its life history, *H. sanguineus* may be available as prey to a wider range of size classes (cohorts) of fishes for longer periods of time than native prey.

In addition to size-mediated relationships between predators and prey, variation in habitat may influence the "catchability" of prey and the apparent preference for specific prey items (Lindholm et al., 1999; Underwood et al., 2004). Physical properties of the habitat can provide a spatial refuge for prey, influencing prey encounter probabilities and predator efficiency (Seitz et al., 2001). Across the intertidal region, *H. sanguineus* is usually found in a narrow range of habitats providing shelter from predation, such as crevices under and between rocks (Ledesma and O'Connor, 2001; Lohrer et al., 2000). However, benthic phase juvenile and adult *H. sanguineus* have been observed across a broad range of habitats in the subtidal and could therefore be subject to variable rates of mortality by crustacean-eating predators based on variation in catchability.

Based on preliminary data from gut contents of crustacean-eating fishes and observations of prey distribution in the field, we hypothesized that *H. sanguineus* is preyed upon preferentially by native fishes. In this study, we conducted a series of prey-preference experiments under controlled laboratory conditions to determine whether crustacean-eating fishes prefer *H. sanguineus* rather than native crab species, and to provide insight into how predator size and habitat type influence prey preference.

2. Materials and methods

T. onitis, *T. adspersus*, and *C. striata* were used as model predators because they have near-shore distributions at relatively high densities (Collette and Klein-MacPhee, 2002), and potentially have the greatest overlap in occurrence with *H. sanguineus*. Fishes were collected from subtidal sand and gravel habitats along the eastern Connecticut coast on LIS (approximately 41.32°N, 72.06°W) using fish traps as well as hook and line methods. Fishes were held in large (2960 L) flow-through tanks with ambient seawater and near-ambient light:dark cycles, where they were fed a combination of pellet feed and live mussels (*Mytilus edulis*) *ad libitum* once daily. Only fish that appeared to be in good health and were actively feeding were used for experiments. Fish were allowed to acclimate to laboratory conditions for at least 7 days prior to experimentation.

Invasive crabs were collected by hand from rocky intertidal shores in the same area. Native mud crab *Panopeus herbstii* and resident green crab *Carcinus maenas* were collected by trap from adjacent tidal sand-mud flats and rocky subsrates. Crabs were held in 37 L flow-through aquaria, and were fed a diet of *M. edulis* each day *ad libitum*. Crabs were allowed to acclimate to laboratory conditions for at least 24 h prior to use in experiments.

Prey selectivity of native fishes was tested under two conditions. To test for the effects of predator size on prey selectivity, small and large *T. onitis* and *T. adspersus* were used as model species. No sediment was used in this experiment, in order to insure that only variation in predator size influenced selectivity. A second set of experiments included substratum treatments to examine the effects of habitat on prey selectivity in small and large *T. onitis* and *C. striata*. *Centropristus striata* were used here instead of *T. adspersus* due to difficulty in capturing the number of large *T. adspersus* sufficient for experimental replication. In all replicates small fish were 8–15 cm total length (TL; mean $TL = 11.9 \pm 1.70$) and large fish were greater than 22 cm TL (mean $TL = 26.5 \pm 4.88$), regardless of species. Individual fish of each size class were offered the following pair-wise combinations of crabs: *H. sanguineus* × *C. maenas*, *H. sanguineus* × *P. herbstii*, and *C. maenas* × *P. herbstii*. All crabs had a carapace width of approximately 8 mm (mean $CW = 7.75 \pm 0.46$) to ensure that predator choice was based on species characteristics and not simply variation in prey size.

Experiments were conducted in flow-through 37 L rectangular tanks, with a grated cover to prevent escape and a curtain around each tank to minimize disturbances and control the photoperiod (14 h light: 10 h dark). For experiments with substrate, 1 L clean beach sand (<1 mm grain size), 1 L clean pebbles (8–16 mm grain size) or 1 L cobble (64–85 mm grain size) was added to the bottom of each tank. Grain size classes are based on the Wentworth scale (Wentworth, 1922). Each treatment type (i.e. pair-wise comparison and substrate type) was replicated thirty times, except when an insufficient number of individual fish in the desired size range were collected. Individual fish were used only once in a set of experiments. A control treatment for each pair-wise comparison contained only crabs to assess loss due to cannibalism and escapement.

Predator size experiments were conducted from July 2006 to November 2006, and habitat experiments were conducted from June 2007 to September 2007. Seawater ranged from 14 to 21 °C and from 26.6 to 27.9 ppt throughout the experiments. One fish of the appropriate size class was placed into each replicate tank. Fish were starved and allowed to adjust to experimental conditions for 24 h. The fish were then netted aside, and 15 individuals of each of the two prey types from one of the pair-wise comparisons