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SELECTION AND AVAILABILITY OF SHELLFISH PREY FOR INVASIVE GREEN CRABS [*CARCINUS MAENAS* (LINNEAUS, 1758)] IN A PARTIALLY RESTORED BACK-BARRIER SALT MARSH LAGOON ON CAPE COD, MASSACHUSETTS

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ABSTRACT European green crabs (*Carcinus maenas*) are voracious, invasive predators of molluscs and their range is expanding throughout the northwest Atlantic Basin. Green crabs rapidly established following the 2002 partial restoration of East Harbor (EH) (42° 03' 33" N, 70° 07' 43" W), a back-barrier salt marsh lagoon within Cape Cod National Seashore, MA, where crabs potentially contribute to abrupt shifts in bivalve abundance and compromise restoration outcomes. Green crab prey preferences and effects on molluscan assemblages at this site have not been documented. Between June and September 2013, the prey selections of green crabs were documented using mesocosm feeding experiments and green crab diet through stomach content analyses. To evaluate prey availability, molluscan assemblage characteristics were also characterized using benthic coring. In the mesocosm experiments, green crabs strongly preferred large softshell clams [*Mya arenaria* (Linnaeus, 1758)] and also chose small *M. arenaria* and Baltic clams [*Macoma balthica* (Linnaeus, 1758)]. Crabs infrequently chose quahogs [*Mercuria mercenaria* (Linnaeus, 1758)], and only small individuals. Six dietary groups were documented in stomachs of crabs captured in the field; arthropods, molluscs, and vegetation were common stomach contents. Twelve molluscan species were detected throughout EH, many of which likely serve as prey for green crabs. Although mollusc abundance in EH has fluctuated because restoration began, the mollusc community remains sufficiently diverse and abundant to provide ample food for green crabs. In this nascent, simplified system, green crabs have few if any predators and thus may exert greater influence as a predator in EH than in other, more well-developed benthic communities.

KEY WORDS: gut contents, mesocosm, molluscs, prey preferences, salt marsh restoration, tidal restriction, *Carcinus maenas*

INTRODUCTION

Salt marshes provide critical ecosystem services such as water quality protection, mitigation of coastal erosion, stabilization of excess water runoff from inland sources, and provision of habitat for diverse and economically important coastal flora and fauna (Carlisle et al. 2002). Over the last few centuries, human-mediated restriction of tidal flow by roads, railroad crossings, dikes, and levees has resulted in ecosystem degradation from nutrient enrichment, changes in salinity and water chemistry, and loss of biodiversity (Carlisle et al. 2002, Raposa & Roman 2003, Portnoy et al. 2005). Coastal habitat degradation creates favorable conditions for the establishment and proliferation of invasive species (Braatz et al. 2007, Cochar et al. 2008, Koch et al. 2009), and human-mediated species introductions are associated with declining habitat quality and biodiversity loss (Tyrrell et al. 2000).

Over the past century, the European green crab (*Carcinus maenas*) (Portunidae) has become one of the most successful invasive predators in U.S. coastal ecosystems (Grosholz & Ruiz 2002). Its ability to tolerate air exposure, starvation, and wide ranges in salinity (4–54 psu) and temperature (0–33°C) allowed this species to survive long voyages in ship ballasts, whereby it was introduced to new areas via marine commerce (Behrens Yamada & Hauck 2001). Green crabs were first documented on the East Coast of the United States in 1817, and is now successfully established on the Atlantic and Pacific coasts of North America, South Africa, South America, Asia, and Australia (Klassen & Locke 2007). They are hardy, voracious

omnivores that can restructure marine benthic communities (Raffaelli et al. 1989, Grosholz et al. 2000, McDonald et al. 2001) and alter ecosystem functioning (Cohen et al. 1995). Stomach content studies document a varied diet that includes annelids (Gee et al. 1985), gastropods (Hughes & Elner 1979, Hadlock 1980), algae (Elner 1981), crustaceans (Ropes 1968), and particularly bivalves (Glude 1955, Cohen et al. 1995, Klassen & Locke 2007). Thus, green crab predation can influence the abundance and distribution of commercially and ecologically important marine species (Leber 1985, Sanchez-Salazar et al. 1987, Raffaelli et al. 1989, Baeta et al. 2006, Pickering & Quijón 2011), and thus may thwart restoration efforts in formerly degraded coastal systems, for example, salt marshes, that are still equilibrating after initiation of restoration.

East Harbor (EH), located within Cape Cod National Seashore (CCNS) on the Cape Cod Peninsula, MA (Fig. 1), is a 291-ha coastal back-barrier salt marsh/lagoon complex undergoing restoration after long-term historical tidal restriction. Since partial restoration began in 2002, salinity has increased substantially and estuarine flora and fauna have successfully established (Thelen & Thiet 2009, Watts et al. 2011, Thiet et al. 2014a). Molluscan assemblages in particular reestablished almost immediately after tidal exchange was restored (Thelen & Thiet 2009), although their abundance has fluctuated substantially since then (Thiet et al. 2014a). By 2009, water chemistry and nekton assemblages indicated that species composition more closely resembled those of an unrestricted estuarine community (Dibble et al. 2015). Nonetheless, challenges persist as the system equilibrates. Severe macroalgal blooms [particularly *Ulva intestinalis* (Linnaeus, 1753)] in 2006–2007 caused extensive seagrass, shellfish, and

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Figure 1. East Harbor back-barrier salt marsh lagoon, North Truro, MA. The three sub-basins are labeled Moon Pond, Main Lagoon, and Northwest Cove. Also note the two culverts, one under Route 6 connecting EH to Cape Cod Bay, and the other connecting Moon Pond to the Main Lagoon and northwest Cove under High Head Road.

finfish die off (Portnoy et al. 2007, Thiet et al. 2014a), and were likely caused by a combination of very high postrestoration softshell clam densities, high late-summer water temperatures, and the absence of algal grazers [e.g., periwinkles, *Littorina littorea* (Linnaeus, 1758)] in areas of the lagoon/marsh complex that still have relatively limited tidal exchange (Smith et al. 2011, Thiet et al. 2014b). Further, the number of invasive European green crabs has increased notably in EH since 2005 (Dibble et al. 2015, H. Bayley, Cape Cod National Seashore, unpublished data). Although invasive green crabs forage broadly, bivalve molluscs make up the largest portion of their diet (Ropes 1968, Grosholz et al. 2000). Thus, intense predation by green crabs could impede restoration efforts (including use for aquaculture) by reducing bivalve abundance

and recovery from losses incurred during the 2006–2007 macroalgal blooms.

Green crab feeding behavior and prey preferences at EH have not been documented. Thus, the aims of this study were to determine the effects of increased green crab abundance on mollusc assemblages at EH, using stomach content analyses from adult crabs captured in the field, as well as mesocosm feeding experiments to discern molluscan prey choices. To characterize the available prey for green crabs throughout EH, molluscan prey abundance, sizes, and distribution at the site were also quantified. Using prey selection information in conjunction with mollusc community characterization, the potential ecological consequences of green crab invasion on mollusc assemblages and benthic restoration outcomes in this system are evaluated.

MATERIALS AND METHODS

Site Description

East Harbor is situated between the Atlantic Ocean and Cape Cod Bay (Fig. 1) in North Truro, MA. Once connected to Cape Cod Bay, the original 300-m inlet to EH was diked in 1868 at its northwest end for the creation of a railway (Portnoy et al. 2005). Tidal restriction reduced salinity and degraded water quality, resulting in the extirpation of native estuarine flora and fauna (Mozgala 1974, Portnoy et al. 2005). In 2002, CCNS and the Town of Truro began restoring EH by opening two clapper valves in a culvert (1.8 × 1.2 m, 213 m long) at the southeastern corner of the marsh that connects the system to Cape Cod Bay (Smith & Medeiros 2013, Thiet et al. 2014a) (Fig. 1). Opening the culvert allowed for seawater exchange, though at a significantly lower level than what flowed through the natural inlet historically (Smith & Medeiros 2013). Despite reduced flow, enough seawater entered the system to rapidly increase salinity and allow an influx of estuarine flora and fauna (Thelen & Thiet 2009, Smith & Medeiros 2013, Thiet et al. 2014a). For example, softshell clams (*Mya arenaria*) reached very high densities (3,200 individuals/m²) in Moon Pond by 2005 (Thelen & Thiet 2009), and the commercially valuable quahog (*Mercenaria mercenaria*) also established in EH in moderate densities following the partial restoration (Thelen & Thiet 2009).

East Harbor is divided into three sub-basins: Moon Pond, the Main Lagoon, and the Northwest Cove (Smith et al. 2011, Thiet et al. 2014a) (Fig. 1). Moon Pond (the main tidal creek) receives the greatest marine influence due to its direct connection to Cape Cod Bay and has the greatest tidal range (~50 cm) and salinity (~30 psu) (Portnoy et al. 2006). Tidal flow is constricted from the tidal creek to the Main Lagoon and the small sub-embayment known as the Northwest Cove by an additional culvert (0.88 m high × 2.2 m wide × 9.5 m long) under High Head Road (Portnoy et al. 2007, Thiet et al. 2014a) (Fig. 1). Salinities currently range from ~20 to 30 psu in the Main Lagoon (Portnoy et al. 2007) and ~15 to 20 psu in the Northwest Cove (Thiet et al. 2014a).

Although mollusc species richness and abundance are greater in EH 14 y after restoration began, they have declined since the first mollusc survey in 2005 (Portnoy et al. 2006, Thelen & Thiet 2009, Thiet et al. 2014a). Further, with increased salinity and benthic abundance and diversity, conditions are now more hospitable to a new assemblage of predators [e.g., Atlantic horseshoe crabs (*Limulus polyphemus*), American eels (*Anguilla rostrata*), moonsnails (*Euspira heros*), and invasive species, including the invasive European green crab (*Carcinus maenas*)]. Green crabs were not observed in EH before the culvert opening in 2002, but were documented in Moon Pond in 2003 (Portnoy et al. 2006), and have been increasing in abundance since 2005 (Dibble et al. 2015, H. Bayley, Cape Cod National Seashore, unpublished data).

Research Design

To evaluate green crab prey selection preferences among three of the most abundant shellfish species in post-restoration EH, laboratory experiments and field observations were conducted from April to September 2013. The availability of

potential molluscan prey was also evaluated by quantifying molluscan species richness, abundance, sizes, and distribution.

Mesocosm Prey Selection Experiment

In July 2013, a laboratory mesocosm experiment was conducted on green crab prey selection in a grow room at the CCNS North Atlantic Coastal Laboratory. In this investigation, green crab prey selection was tested using three mollusc species common in EH: softshell clams (*Mya arenaria*), Baltic clams (*Macoma balthica*), and quahogs (*Mercenaria mercenaria*) (Thelen & Thiet 2009, Thiet et al. 2014a). All three species are common prey items for green crabs (Glude 1955, Ropes 1968, Richards et al. 1999, Hiddink et al. 2002, Floyd & Williams 2004, Miron et al. 2005, Donahue et al. 2009) and their consistent presence and wide distribution throughout EH following restoration (Thiet et al. 2014a), as well as their potential recreational and commercial value for shell fishing (Glude 1955, Ropes 1968, Lafferty & Kuris 1996) at this site, made them ideal mollusc species for the mesocosm prey preference experiment.

Experimental mesocosms were composed of 10-gallon glass aquaria (59.0 × 22.0 × 33.0 cm), which were filled with approximately 4 cm of sand and 4 cm of water collected from Moon Pond (Thiet et al. 2014b). Sand was collected from the nearby Province Lands sand dunes, sieved through 1-mm mesh, and air-dried to ensure no surviving macroinvertebrates persisted before being placed in mesocosms. Free-floating nekton was removed from the water but the water was not filtered. One air stone (6" Top Fin; Franklin, WI) positioned at the back of each tank kept water aerated, and fans positioned over tanks facilitated air–water gas exchange to cool tanks as summer temperatures increased. Ten mesocosms were established: six experimental mesocosms with crabs (obtained from pitfall traps) and four controls without crabs. Experimental mesocosms were interspersed between controls, and the sides of tanks were lined with white paper to eliminate visual stimuli among tanks (Abramson & Feinman 1990). To prevent crabs from escaping, a fine grade mesh (The New York Wire 36 in. × 7 ft. Fiberglass Screen Mesh, NY Wire Company, Hanover, PA) was outfitted over each experimental tank.

To encourage crabs to feed, natural summer light conditions were simulated in mesocosms. A 60-W fluorescent light bulb (Soft White, Ecosmart, Atlanta, GA) was positioned between every two aquaria, and was maintained on a timer programmed to keep a constant photoperiod of 14-h light/10-h dark (Miron et al. 2005). Light intensity was kept relatively low by lighting only the front half of the mesocosm and leaving the back in semidarkness, thereby providing a refuge for the crabs and reducing physiological and behavioral stress from overexposure to light.

The mesocosm experiment was conducted over a 5-wk period from July 1 to July 30, 2013, with two experimental runs per week (total: 10 experimental runs). Crabs were collected every 3–4 days from June 27 to July 25, 2013 from pitfall traps in Moon Pond and held in holding tanks with approximately 5 cm of water. Crabs were separated from each other by thick plastic dividers to prevent aggression that could cause shell damage and cannibalism. To avoid potential variation in foraging that could result from behavioral and morphological differences associated with age and sex, only adult male crabs between 6.4 and 8.6 cm carapace width, with

two intact chelae, were used (Elner & Hughes 1978, Hill et al. 1991, Abello et al. 1994, Mascaro & Seed 2001, Matheson & Gagnon 2012). To standardize hunger levels and ensure motivation to forage, crabs were starved for 72 h before each experimental run was initiated (Chakravarti & Cotton 2014). This was enough time for crabs to evacuate their digestive systems without inducing the large-scale physiological changes of starvation (Wallace 1973). Only green-phase *Carcinus maenas* were used for this experiment to minimize foraging variability due to physiological differences associated with color morphology (Reid et al. 1997). Despite their common name, green crabs actually range in coloration from pale green to deep red during different molting phases (Lee et al. 2003). Male red phase crabs are larger and stronger and have a competitive advantage over green phase crabs for habitat, mates, and prey (Reid et al. 1997; Kaiser et al. 1990), but green phase crabs are better osmoregulators and oxyregulators (Reid & Aldrich 1989, Reid et al. 1997) and therefore better tolerate environmental stress (Reid et al. 1989).

Molluscs were collected to use as prey for the mesocosm experiment in May–July 2013. In a pilot mesocosm study conducted in June 2013, *Carcinus maenas* consumed varying sizes of *Mya arenaria*, *Macoma balthica*, and *Mercenaria mercenaria*, and thus these sizes were used as a guideline for the feeding preference experiments. Individual prey items of the desired size ranges (small/large) were randomly sampled in each sub-basin, and were *M. arenaria* (small $\sim 3.5 \pm 0.5$ cm, large $\sim 5.8 \pm 0.5$ cm), *M. balthica* (small $\sim 2.2 \pm 0.5$ cm, large $\sim 2.7 \pm 0.5$ cm), and *M. mercenaria* (small $\sim 1.5 \pm 0.5$ cm, large $\sim 2.3 \pm 0.5$ cm). All prey items collected were maintained in three aerated 10-gallon holding tanks with 5 cm of sand substrate and 5 cm of unfiltered water from Moon Pond. Water in holding tanks was replaced with fresh water from Moon Pond every other day to provide algae as a constant food source. Six hours prior to each run, one bivalve from each size class (small and large) and species (*M. arenaria*, *M. balthica*, and *M. mercenaria*) was selected and measured, and then the six prey items were added to each mesocosm including controls. The substrate was deep enough to allow molluscs to completely cover themselves and extend their siphons without being exposed (Miron et al. 2005, Thiet et al. 2014b). Holes were dug to gently insert any molluscs into the substrate that did not burrow within the 6-h period.

Immediately prior to each run, six crabs were selected for use in our experimental mesocosms (the four control mesocosms did not have crabs). Each crab was inspected, any damage was noted, carapace width and chela height were measured (in centimeters), and handedness (right or left primary crusher claw) was recorded. One crab (6.4–8.6 cm carapace width) was then placed into each experimental mesocosm and given 24 h to forage. Crab behavior was directly observed for the first 6 h of each run, a period that coincided with the end of the 14-h light photoperiod and a time when crustacean foraging is expected to be high due to reduced predation risk in the wild (Hayden et al. 2007). Each time the green crab in each tank actively located, unearthed, opened, crushed, or consumed a prey item (*Mya arenaria*, *Macoma balthica*, and/or *Mercenaria mercenaria*) was considered a feeding event (Fuzessery & Childress 1975, Pearson et al. 1979, Schmitt & Ache 1979, Zimmer-Faust et al. 1996) and was subsequently treated as a replicate in our prey preference analysis. Crabs were permitted to forage without light or an observer for the remaining 18 h of the 24-h run.

At the end of each 24-h experimental run, crabs and water were removed from mesocosms and substrate was inspected for all visible prey items. The sizes and species of all consumed molluscs were confirmed by sieving (1-cm mesh size) each mesocosm's substrate and measuring the remaining molluscs. Any uneaten prey were counted and measured, and then returned to the holding tanks. Because of the patchy location of molluscan prey of the appropriate size classes in the field, prey from controls and any uneaten prey from experimental tanks were sometimes used in subsequent runs; when this occurred, prey items were randomly distributed among mesocosms and treatment groups (treatment and control), that is, prey items were not used in the same mesocosms between runs.

The volume of sand substrate in each mesocosm remained constant, but was incrementally replaced with substrate from Moon Pond if lost during sieving. Salinity was recorded at the beginning of each run using a handheld refractometer and temperature readings were collected every 6 h over each run. Water temperature in mesocosms varied between 19.0°C and 28.2°C, and ambient air temperatures varied between 20.6°C and 31.7°C. Each crab was used only once in the experiment, and water and prey items were replaced for each new run.

Stomach Content Analysis

Green crab stomach content analysis was conducted using crabs collected from EH between August 15 and September 27, 2013. For a concurrent study of *Carcinus maenas* population structure and distribution in EH (Conkerton 2015), *C. maenas* were captured via 10 pitfall traps placed randomly 1 m from the shoreline in each sub-basin of EH. Crabs were collected from pitfall traps approximately once weekly during the sample period and all crabs captured were retained for stomach content analysis. Each pitfall trap was a 20-l polyethylene bucket (0.3 m diameter \times 0.35 m deep) buried flush with the sediment surface. All captured crabs measuring >3.0 cm, regardless of sex or molt stage, were retained for stomach content analysis, frozen for at least 48 h, and then defrosted for at least 30 min immediately prior to dissection (Donahue et al. 2009). For each crab dissected, color, sex, reproductive condition (occurrence of ovigerous females), molt stage, damaged/missing body parts, location and date of collection, chela height (in centimeters), and carapace width (in centimeters) were recorded. Crabs were dissected down to their cardiac stomachs, placed in individually labeled vials, and then frozen for later analysis.

Diet characterization of *Carcinus maenas* in EH was based on the stomach contents of 96 crabs. Each stomach was visually assessed for fullness and ranked on a scale of 1–4: 1 (0%–25% full), 2 (25%–50% full), 3 (50%–75% full), and 4 (75%–100% full) (Mantelatto & Petracco 1997, Edgerly 2006). The size of each cardiac stomach was measured to the nearest 0.1 cm, and then the stomach contents were flushed into a shallow plastic dish with tap water (Haefner 1990). Forceps were used to push food items over each of the 49 grid intersections imbedded in the bottom of the plastic dish and the point intercept method was used to ensure each item was recorded only once. One additional identification point was added to account for 50 items from each stomach; when a stomach had fewer than 50 items, all material was identified (Edgerly 2006).

Stomach contents were identified to the lowest possible taxonomic level using a VWR Vista Vision binocular dissecting microscope (Motic, Richmond, BC, Canada) (Grosholz et al.

2000). When identification of a food item was uncertain, a binocular Meiji Techno Zoom Stereo EMZ camera microscope (Meiji Techno America, San Jose, CA) was used to capture images for further analysis. For some food items, mastication into discolored amorphous material made it difficult to assign items to a definite species (Taylor 2004), but food could usually be identified to a more general taxonomic group (Elnor 1981). Some key identifying features used were the presence of jaws in Nereida, apical whorls in gastropods, cylindrical body segments in amphipods and isopods, and the presence of intact gills, stomachs, seta, and carapace in crabs (Haefner 1990). Diet components were assigned to the following categories: Annelida, Arthropoda, Chlorophyta, Mollusca, Organic Matter, and Unidentified Material. "Organic matter" was obvious, organic hard and soft material for which a taxonomic category could not be identified. All unrecognizable, amorphous debris was assigned to the category "Unidentified Material."

After stomach contents were identified, the relative number of stomachs occupied by each food item in the stomach was estimated using Frequency of Occurrence (FOO), defined as the number of stomachs containing one or more items of each food category, expressed as a percentage of all stomachs containing food (Hyslop 1980, Wear & Haddon 1987). Although this method gives little indication of the relative amount or bulk of each food category in the stomach, it does provide a qualitative picture of the prey spectrum contained within each stomach (Crisp 1963, Fagade & Olaniyan 1972, Hyslop 1980).

The percent presence of each prey group was also quantified to determine how common a prey item was across *Carcinus maenas* individuals (the total number of prey items in a sample expressed as a percentage for all stomachs; modified from Stevens et al. 1982). In addition, the average number of prey groups per crab was quantified to describe individual crab diet diversity in the short term (Stevens et al. 1982, Edgerly 2006). All diet diversity calculations were made using only the crab stomachs that contained food; empty stomachs were excluded from our diet diversity analysis, although the number and percentage of empty stomachs were calculated (Stevens et al. 1982).

Molluscan Assemblage Characterization

Between mid-August and September 2013, mollusc species richness, abundance, and distribution were characterized at 47 sampling points throughout EH used in earlier mollusc studies by Thelen and Thiet (2009) and Thiet et al. (2014a): 19 in Moon Pond, 4 in the Northwest Cove, and 24 in the Main Lagoon. Because digging and sieving were difficult in deep water (2 m) at the interior of the lagoon, some sampling points were adjusted to be closer to the shoreline where water was <1 m deep (Thelen & Thiet 2009). Because relatively consistent gradients in salinity, temperature, and dissolved oxygen occur with distance from the culvert connecting EH to Cape Cod Bay, stratified random sampling was used to capture a representative sample of molluscan assemblages in each of the three sub-basins (Portnoy et al. 2005, Thelen & Thiet 2009).

To quantify mollusc abundance (measured as individuals/m²), five benthic cores (10 cm diameter × 20 cm depth) were collected within a 0.5-m² quadrat at each sample point and sieved through 1-mm mesh to collect large molluscs, and then the remaining sediment in the quadrat was searched for 2 min to ensure unbiased detection of individual molluscs (Thelen & Thiet 2009). From these data, mollusc abundance (individuals/m²) in each sub-basin was calculated by extrapolating up to 1 m²

(total individuals per sample × 2). All living molluscs were identified to species and measured (in centimeters).

Statistical Analysis

Differences in green crab prey selection in our laboratory mesocosms were tested in three ways: by species (*Mya arenaria* versus *Macoma balthica* versus *Mercenaria mercenaria*), by size overall (small versus large), and by size within each species (i.e., small versus large *M. arenaria*, etc.), treating each feeding event as one replicate in the applicable treatment group (e.g., one feeding event on *M. arenaria*). Prey selection data were proportional (e.g., the proportion of individual *M. arenaria* consumed given the number of *M. arenaria* individuals offered), so data were arcsine-transformed prior to analysis to make the distribution more appropriate for traditional analysis of variance. Transformation did not improve data distribution or meet the assumptions necessary for use of parametric statistics; thus, nonparametric tests were performed on the arcsine-transformed data. Nonparametric Kruskal–Wallis analyses were used to test which species of prey green crabs preferred (*M. arenaria* versus *M. balthica* versus *M. mercenaria*), and to compare green crab prey preferences within all small individuals of each species and within all large individuals of each species. Where differences among species preferences were detected, Tukey's honest significant difference post hoc tests were used for mean comparisons. Size preference within species (e.g., small versus large *M. arenaria*) was tested using a Chi-square test for each prey species.

To analyze stomach content data, a Chi-square contingency table was used with the six content categories observed: Annelida, Arthropoda, Chlorophyta, Mollusca, Organic Matter, and Unidentified Material. A Likelihood ratio Chi-square (G-test) of independence was performed to evaluate the association between FOO and the sub-basin in which crabs were captured, crab sex, and crab size. The same test was used to evaluate the association between stomach fullness and the sub-basin in which crabs were captured, crab sex, and crab size; for purposes of the Chi-square analysis, crab sizes were categorized as "medium" (4.0–5.9 cm) and "large" (≥6.0 cm).

Finally, mollusc species richness, abundance, and size were compared among the three sub-basins of EH. Only five species were encountered consistently enough to warrant detailed analyses of their abundance: *Mya arenaria*, *Macoma balthica*, *Mercenaria mercenaria*, *Gemma gemma* (Totten, 1834), and *Tritia obsoleta* (Say, 1822). Species richness, abundance, and size data were non-normally distributed and data transformation did not improve normality, so nonparametric Kruskal–Wallis tests were used to determine if significant differences existed in mollusc species richness, abundance, and size among the three sub-basins. Tukey's honest significant difference post hoc tests were used for mean comparisons where significant differences among sub-basins were detected.

All data were analyzed using JMP 9.0.2 statistical software (SAS Institute, Cary, NC, 2010), and statistical significance was determined at $\alpha \leq 0.05$.

RESULTS

Green Crab Prey Selection

Green crab prey selection preferences were compared among three abundant shellfish species in EH by observing their choices

in a laboratory experiment, and by dissecting the stomachs of adult green crabs captured in pit traps at the study site.

Laboratory Mesocosm Study

The 60 individual *Carcinus maenas* used in the mesocosm experiment consumed a total of 179 individual bivalves of the 360 total bivalves presented to them in the mesocosms, and crabs showed statistically significant differences in their preferences for *Mya arenaria*, *Macoma balthica*, and *Mercenaria mercenaria* ($\chi^2 = 62.22$, $df = 2$, $P < 0.0001$). Post hoc mean comparisons revealed significant differences in the frequency with which green crabs chose *M. arenaria* versus *M. mercenaria* ($P < 0.0001$), *M. arenaria* versus *M. balthica* ($P = 0.0007$), and *M. balthica* versus *M. mercenaria* ($P < 0.0001$). Green crabs preferred *M. arenaria* first (mean \pm one SE: 0.78 ± 0.39 individuals consumed), *M. balthica* second (mean 0.55 ± 0.05 individuals consumed), and *M. mercenaria* third (mean 0.18 ± 0.04 individuals consumed).

When evaluating which prey size green crabs preferred overall (i.e., large versus small prey within all three prey species combined), *Carcinus maenas* clearly preferred small prey, and differences in small prey consumption differed significantly among small *Mya arenaria*, *Macoma balthica*, and *Mercenaria mercenaria* ($\chi^2 = 20.91$, $df = 2$, $P < 0.0001$). Specifically, crabs chose small *M. arenaria* significantly more than small *M. mercenaria* (mean frequencies: 0.66 ± 0.06 versus 0.25 ± 0.06 , respectively; $P < 0.0001$), and small *M. balthica* (mean frequency: 0.48 ± 0.07) significantly more than small *M. mercenaria* ($P = 0.02$). Crabs did not show a statistically significant preference between small *M. arenaria* and small *M. balthica* ($P = 0.09$). Similarly, green crabs chose large individuals of all prey species at significantly different frequencies ($\chi^2 = 72.75$, $df = 2$, $P < 0.0001$), with large *M. arenaria* (mean frequency: 0.88 ± 0.80) being chosen significantly more frequently than large *M. balthica* (mean frequency: 0.62 ± 0.06) and large *M. mercenaria* (mean frequency: 0.12 ± 0.04) ($P = 0.0006$ and $P < 0.0001$, respectively). Crabs also significantly preferred large *M. balthica* to large *M. mercenaria* ($P < 0.0001$).

Tests of green crab prey size preferences within each prey species (e.g., small versus large *Mya arenaria*) showed that *Carcinus maenas* strongly preferred large *M. arenaria* over small *M. arenaria* (mean frequencies 0.88 ± 0.04 and 0.66 ± 0.06 , respectively; $\chi^2 = 8.01$, $df = 1$, $P = 0.005$), but crabs did not show a preference between large and small *Macoma balthica* (mean frequencies: 0.62 ± 0.06 and 0.48 ± 0.06 , respectively; $\chi^2 = 2.14$, $df = 1$, $P = 0.14$). Crabs also strongly preferred small over large *M. mercenaria*, and the difference was nearly significant (mean frequencies: 0.12 ± 0.04 and 0.25 ± 0.06 , respectively; $\chi^2 = 3.53$, $df = 1$, $P = 0.06$).

Stomach Content Analysis

Of 96 adult *Carcinus maenas* stomachs dissected, 77 (80%) were from adult males (M) and 19 (20%) were from adult females (F). Twenty-seven percent (F = 4, M = 22) of stomachs were completely empty. Of the 70 green crabs with food in their stomachs, 80% had a stomach fullness rating of 1 (0%–25%, F = 14, M = 42) and 10% had a fullness rating of 2 (25%–50%, F = 1, M = 6). Only one male crab had a stomach fullness rating of 3 (50%–75%), and six male crabs (8.57%) had a stomach fullness rating of 4 (75%–100%).

Five hundred ninety-one individual prey items representing six groups were identified in the 70 *Carcinus maenas* stomachs that contained food (Table 1). Of the six groups, fragments of Organic Matter were found in 39 stomachs and had the highest FOO, making up 56% of the total stomach contents. After Organic Matter, the category with the second highest FOO (50%) was Arthropoda, which was found in 35 stomachs. Mollusca had 27% FOO and was found in 19 crab stomachs (Table 1).

Between one and six stomach content groups were observed in each green crab stomach (Fig. 2). The average number of groups represented in a single crab stomach was 3.5 ± 0.76 , and the number of food taxa per stomach generally declined with a decrease in stomach fullness. Forty-three percent of crab stomachs contained only one food item and were only 25% full, and those items were usually either Mollusca or Organic Matter. Only one crab had a diet diversity of six taxonomic groups, and that stomach was completely full.

Relationships between stomach fullness and the sub-basin in which crabs were collected, crab sex, and crab size were evaluated (Table 2). Crabs captured in Moon Pond had the fullest stomachs overall, although stomach fullness was not significantly related to the sub-basin where crabs were collected (likelihood ratio $\chi^2 = 1.72$, $df = 6$, $P = 0.94$). Male stomachs tended to have a higher fullness rating than females but this was not a significant difference (likelihood ratio $\chi^2 = 4.01$, $df = 3$, $P = 0.25$) and could be due to the fact that four times as many male than female crabs were evaluated. Stomach fullness was not significantly related to crab size (medium: 4.0–5.9 cm; large: >6.0 cm) (likelihood ratio $\chi^2 = 1.79$, $df = 3$, $P = 0.61$) (Table 2).

Relationships between the FOO of stomach content categories and the sub-basin in which crabs were captured, crab sex, and crab size were also evaluated (Table 3). FOO for stomach contents significantly differed among the three sub-basins where crabs were captured (likelihood ratio $\chi^2 = 23.04$, $df = 10$, $P = 0.01$). Mollusca occurred most frequently in stomachs from Moon Pond (FOO in Moon Pond: 13%) (Table 3).

Stomach contents did not differ significantly between male and female crabs (likelihood ratio $\chi^2 = 4.10$, $df = 5$, $P = 0.53$). The category of greatest interest, Mollusca, was present in about 14.66% of male stomachs and only 6.90% of female stomachs

TABLE 1.

The relative importance of food types when analyzed by their % FOO within crab stomachs from EH, North Truro, MA. FOO = the number of stomachs containing one or more individuals of each food category, expressed as a percentage of all stomachs containing food. We dissected 70 green crab stomachs ranging from 0.7 to 2.0 cm long.

Food item	Number of stomachs		FOO (%F)
	where food items occurred	Number of individual food items found	
Annelida	4	6	5.71
Arthropoda	35	204	50.00
Chlorophyta	29	99	41.43
Mollusca	19	85	27.14
Organic Matter	39	145	55.71
Unidentified	19	52	27.14
Material			

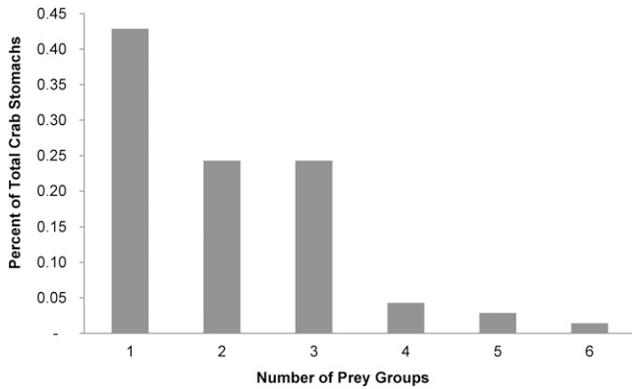


Figure 2. The average number of prey groups (1–6) in each of 70 *Carcinus maenas* stomachs that contained food. We grouped prey items into six categories: Annelida, Arthropoda, Chlorophyta, Mollusca, Organic Matter, and Unidentified Material. The higher the number of prey groups represented within a stomach, the greater the individual crab diet diversity.

(Table 3). Similarly, FOO of stomach contents did not differ significantly between large- and medium-sized crabs (likelihood ratio $\chi^2 = 2.96$, $df = 5$, $P = 0.70$). Large-sized crabs consumed only slightly more Mollusca (14.29%) than did medium crabs (11.48%) (Table 3). It is possible that some of the Organic Matter observed was mollusc tissue, as green crabs tear mollusc flesh into small bits before consuming; thus, the frequency of Mollusca stomach contents may be an underestimate.

Mollusc Assemblage Characteristics

A total of 12 mollusc species were observed in all three sub-basins in 2013: 10 species in Moon Pond, eight in the Main Lagoon, and two in the Northwest Cove (Conkerton 2015). Mollusc species richness did not differ among Moon Pond, the Main Lagoon, and the Northwest Cove ($\chi^2 = 3.82$, $df = 2$, $P = 0.15$). Of all the mollusc species observed, only three have been

encountered in EH every sampling year since 2005: *Mya arenaria*, *Macoma balthica*, and *Mercenaria mercenaria* (Conkerton 2015). Three species were detected in 2013 that were not detected in 2011: *Euspira heros* (Say, 1822) (northern moon snail), *Gemma gemma* (amethyst gem clam), and *Geukensia demissa* (Dillwyn, 1817) (ribbed mussel) (Conkerton 2015).

A total of 515 individual molluscs were detected during the sampling period, and mollusc abundance did not differ significantly among Moon Pond, the Main Lagoon, and the Northwest Cove in 2013 ($\chi^2 = 4.55$, $df = 2$, $P = 0.10$). Softshell clam was the only mollusc species detected every sampling year in each sub-basin, but its abundance has decreased in Moon Pond from 3,178.33 ($\pm 1,809.94$)/m² in 2005 to 2 (± 0.82)/m² in 2013, and in the Main Lagoon from 2,971.09 (± 726.64)/m² in 2005 to 2.58 (± 1.01)/m² in 2013 (Thiet et al. 2014a, Conkerton 2015). Baltic clams were recorded in the same abundances in 2005 and 2013 (mean 0.11 \pm 0.11/m² each year).

Mollusc sizes did not differ significantly among Moon Pond, the Main Lagoon, and the Northwest Cove in 2013 ($\chi^2 = 0.21$, $df = 2$, $P = 0.90$). The size of *Gemma gemma* ranged from mean of 0.08 (± 0.03) cm in Moon Pond to 0.06 (± 0.03) cm in the Main Lagoon (Conkerton 2015). Softshell clams were biggest in the Northwest Cove (mean 2.43 \pm 1.43 cm), and *Macoma balthica* ranged from 0.16 (± 0.16) cm in Moon Pond to 0.84 (± 0.21) cm in the Main Lagoon. Quahogs ranged from 1.02 (± 0.41) cm in Moon Pond to 0.49 (± 0.25) cm in the Main Lagoon (Conkerton 2015).

DISCUSSION

The results from this study concur with other studies (e.g., Elner 1981) in which green crabs strongly preferred both small and large, soft-shelled *Mya arenaria* over other mollusc species; they also preyed upon northern quahogs *Mercenaria mercenaria*, but were more likely to target smaller juveniles than larger adults. The softshell clams *M. arenaria* has been encountered in Moon Pond every sampling year since 2005, and in some years has

TABLE 2.

Results from Likelihood ratio Chi-square tests (G-test) of independence to test for relationships between stomach fullness rating and sub-basin of EH in which crabs were collected, crab sex, and crab size. Of the 96 crabs dissected, 70 contained food, and these were ranked into fullness categories of 1–4. *N* = number of crabs collected that fell into each fullness category.

Variable	Stomach fullness rating				Total	χ^2 , <i>P</i>
	Fullness categories					
	1 (0%–25%) <i>N</i> (%)	2 (25%–50%) <i>N</i> (%)	3 (50%–75%) <i>N</i> (%)	4 (75%–100%) <i>N</i> (%)		
Sub-basin						
Moon Pond	39 (81.25)	4 (8.33)	1 (2.08)	4 (8.33)	21 (30.00)	1.72
Lagoon	16 (76.19)	3 (14.29)	0 (0.00)	2 (9.52)	48 (68.57)	0.94
NW Cove	1 (100.00)	0 (0.00)	0 (0.00)	0 (0.00)	1 (1.43)	
Total	56 (80.00)	7 (10.00)	1 (1.43)	6 (8.57)	70	
Sex						
Male	42 (76.36)	6 (10.91)	1 (1.82)	6 (10.91)	15 (21.43)	4.01
Female	14 (93.33)	1 (6.07)	0 (0.00)	0 (0.00)	55 (78.57)	0.25
Total	56 (80.00)	7 (10.00)	1 (1.43)	6 (8.57)	70	
Size						
Medium	24 (82.76)	2 (6.90)	0 (0.00)	3 (10.34)	29 (41.43)	1.79
Large	32 (78.05)	5 (12.20)	1 (2.44)	3 (7.32)	41 (58.57)	0.61
Total	56 (80.00)	7 (10.00)	1 (1.43)	6 (8.57)	70	

TABLE 3.

Results from Likelihood ratio Chi-square tests (G-test) of independence to test for relationships between the prey groups found in crab stomachs and the sub-basin in which crabs were collected, crab sex, and crab size. Of the 96 crabs dissected, 70 contained food, and these were ranked into fullness categories of 1–4. Stomach contents were grouped into six categories: Annelida, Arthropoda, Chlorophyta, Mollusca, Organic Matter, and Unidentified Material. *N* = number of crabs collected that fell into each FOO category, and (%) is FOO.

Variable	FOO						Total	χ^2, P
	Prey Categories							
	Annelida <i>N</i> (%)	Arthropoda <i>N</i> (%)	Chlorophyta <i>N</i> (%)	Mollusca <i>N</i> (%)	Organic Matter <i>N</i> (%)	Unidentified material <i>N</i> (%)		
Sub-basin								
Moon Pond	1 (1.02)	22 (22.45)	17 (17.35)	13 (13.27)	36 (36.73)	9 (9.18)	98 (67.59)	23.04
Main Lagoon	3 (6.98)	12 (27.91)	11 (25.58)	5 (11.63)	3 (6.98)	9 (20.93)	43 (29.66)	0.01
NW Cove	0 (0.00)	1 (25.00)	1 (25.00)	1 (25.00)	0 (0.00)	1 (25.00)	4 (2.76)	
Total	4 (2.76)	35 (24.14)	29 (20.00)	19 (13.10)	39 (26.90)	19 (13.10)	145	
Sex								
Male	4 (3.45)	26 (22.41)	22 (18.97)	17 (14.66)	32 (27.59)	15 (12.93)	116 (80.00)	4.10
Female	0 (0.00)	9 (31.03)	7 (24.14)	2 (6.90)	7 (24.14)	4 (13.79)	29 (20.00)	0.53
Total	4 (2.76)	35 (24.14)	29 (20.00)	19 (13.10)	39 (26.90)	19 (13.10)	145	
Size								
Medium	1 (1.64)	12 (19.67)	15 (24.59)	7 (11.48)	17 (27.87)	9 (14.75)	84 (57.93)	2.96
Large	3 (3.57)	23 (27.38)	14 (16.67)	12 (14.29)	22 (26.19)	10 (11.90)	61 (42.07)	0.70
Total	4 (2.76)	35 (24.14)	29 (20.00)	19 (13.10)	39 (26.90)	19 (13.10)	145	

been the most abundant mollusc species in EH (Thelen & Thiet 2009, Thiet et al. 2014a). Large *M. arenaria* shells were frequently observed littering the substrate of Moon Pond, and crabs collected there contained the most food and the most molluscan prey in their stomachs (finding identifiable *M. arenaria* shell fragments in a stomach is unlikely). In addition, mollusc species richness and abundance were higher overall in Moon Pond compared with the other sub-basins, which may, in part, support the high green crab abundance observed there (Conkerton 2015). Specifically, Moon Pond contained high densities of *M. arenaria*, *M. balthica*, *M. mercenaria*, *Tritia obsoleta*, and *Mytilus edulis* (Linnaeus, 1758), all species that green crabs forage extensively (Ropes 1968, Walne & Dean 1972, Dare & Edwards 1976, Davies et al. 1980, Dare et al. 1983, Sanchez-Salazar et al. 1987, Grosholz & Ruiz 1995). Although the Main Lagoon had lower molluscan species richness and abundance than Moon Pond, it contained moderate to high densities of *Gemma gemma*, *M. balthica*, and *M. arenaria*, and small numbers of other mollusc species, for example, *T. obsoleta*, *M. mercenaria*, *Mulinia lateralis* (Say, 1822), *Petricola pholadiformis* (Lamarck, 1818), and *Spisula solidissima* (Dillwyn, 1817) (Conkerton 2015).

Although green crabs in mesocosms preferred both small and large *Mya arenaria*, they consumed small *M. arenaria* and small *M. balthica* at similar frequencies. The Baltic clam is a highly desirable prey species for green crabs (van der Veer et al. 1998, Hiddink et al. 2002, Griffiths & Richardson 2006), occurred in the highest abundance in the Main Lagoon, and has been encountered consistently in the Main Lagoon since 2007 (Thiet et al. 2014a). Despite the high abundance of these two species and moderate abundances of other desirable mollusc prey species in the Main Lagoon, fewer than half the crabs collected from that sub-basin contained food in their stomachs, and only a small percentage of those contained tissue that was

definitively Mollusca. Thus, it is uncertain whether green crab abundance in the Main Lagoon can be explained by prey presence there. It is possible that green crabs are constrained to foraging in mollusc-dense areas of Moon Pond, and then move into the Main Lagoon via the culvert under High Head Road.

Green crab diet preferences and ecological impacts are qualitatively similar on different continents and ocean basins (Grosholz & Ruiz 1996), which may allow predictions of the influence of their presence. Specifically, green crabs show a strong preference for Mollusca prey, primarily bivalves, both in their native Europe and across their expanded range in eastern North America, western North America, and southern Africa (Grosholz & Ruiz 1996). In eastern North America, precipitous declines in the abundance of the commercial *Mya arenaria* during the first half of the 20th century correlated with the northeastward expansion of green crabs through Maine and maritime Canada (Glude 1955, Ropes 1968); at one site, clam abundance declined by 50% in only 4 y (Glude 1955). Green crabs also reduce populations of bivalves in invaded areas of western North America, where the resulting severe declines in benthic invertebrates may potentially have multi-trophic effects on shorebirds and fishes (Grosholz & Ruiz 1996), phytoplankton biomass and productivity, nutrient availability, sediment biogeochemistry, and the pelagic food web (Prins et al. 1998, Kimbro et al. 2009). In regions where green crabs occur, their effects are more pronounced in lower-energy habitats such as protected embayments (i.e., in contrast to exposed rocky shores; Muntz et al. 1965, Menge 1976, Grosholz & Ruiz 1996). Although little is known about the potential multitrophic effects of green crabs in eastern North America, the similarity in their diet and feeding behavior between eastern and western North America (Grosholz & Ruiz 1996) suggests that predation on bivalves may have

multitrophic effects in protected embayments of eastern North America as well.

Results from stomach content analyses concurred with other studies in which diet composition varied by crab size (Ropes 1968, Elner 1980). The stomachs of large-sized *Carcinus maenas* captured contained more Annelida, Arthropoda, and Mollusca, whereas small- and medium-sized crabs contained more Chlorophyta, Organic Matter, and Unidentified Material (likely animal material). Crab foraging behavior and prey choice are often a function of claw morphology and size (Reid et al. 1997) and relate to the ease with which prey can be opened (Kaiser et al. 1990, Trussell & Nicklin 2002, Cotton et al. 2004). Larger crabs have stronger crushing force of their chelae, which increases with body size (Taylor et al. 2009).

In this study, green crab diet varied between the sexes, and although the difference was not statistically significant, it may be ecologically significant. Compared with males, female stomachs contained more Arthropoda, Chlorophyta, and Unidentified Material, whereas male stomachs had more Mollusca, Organic Material, and Annelida. The differences in diet may partly be explained by sexual dimorphism, with male *Carcinus maenas* typically being larger than females, which were observed at our study site. Chela height and mechanical advantage are significantly greater in males than in females of comparable carapace width (Lee & Seed 1992; but see Spooner et al. 2007). The high male:female ratio at this site (Conkerton 2015), combined with the observation that male stomachs contained more molluscs, suggests that *C. maenas* likely reduces mollusc abundance at this site.

Molluscs can evade predation by using locomotion (avoidance) and armor (e.g., *Mercenaria mercenaria*; Vermeij 1987) and by burrowing deeply (e.g., *Mya arenaria* and *Macoma balthica*; Whitlow et al. 2003). Nonetheless, despite that green crabs typically only dig a few centimeters deep, adult crabs have been observed digging pits 15–23 cm deep to extract large clams (Smith & Chin 1951, Dow & Wallace 1952, Ropes 1968, Lindsay & Savage 1978). Sheer size can also be a deterrent, for example, at EH, the large sizes of *M. mercenaria* found in Moon Pond (>6.0 cm) are likely too difficult for green crabs to open. Walton et al. (1999) found that *M. mercenaria* over 1.8 cm

obtained refuge from predation by size, although crabs in our mesocosm studies consumed *M. mercenaria* up to 2.2 cm. To avoid claw damage (Juanes 1992) and prolonged exposure to predators (Elner & Hughes 1978, Hughes & Seed 1981, Ameyaw-Akumfi & Hughes 1987) crabs usually select small prey that can be quickly crushed. Thus, the smaller sizes of *M. arenaria*, *M. balthica*, and *M. mercenaria* in Moon Pond and the Main Lagoon are likely most vulnerable to green crab predation.

To ensure the establishment and persistence of robust benthic and halophyte communities in natural and restored salt marshes, all efforts should be made to retain adequate tidal exchange with adjacent bays and to promote diverse, multitrophic assemblages of marine flora and fauna. Although tidal exchange may introduce green crabs into systems where they were previously absent, sufficient tidal exchange can also introduce predators on green crabs. At EH, opening a larger, unobstructed channel to Cape Cod Bay would allow large fish predators [e.g., Winter flounder *Pseudopleuronectes americanus* (Walbaum, 1792), seaboard goby *Gobiosoma ginsburgi* (Hildebrand and Schroeder, 1928), and striped bass *Morone saxatilis* (Walbaum, 1792)] into the system that could reduce green crab abundance; North American river otters [*Lontra canadensis* (Schreber, 1777)] have recently been observed in the system and likely consume numerous green crabs. Assemblages of higher native biodiversity likely increase ecosystem resilience to invaders (Shea & Chesson 2002, Jensen et al. 2007), although lower-diversity systems may be resilient against invasive species if they contain a highly effective, native, generalist predator or competitor (Crawley et al. 1999). Further, mollusc diversity in both natural and restored salt marshes should be a priority for ongoing monitoring, as mollusc communities are infrequently monitored in restored coastal systems (Thiet et al. 2014a).

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