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Seasonal catch, size, color, and assessment of trapping variables for the European green crab *Carcinus maenas* (Linnaeus, 1758) (Brachyura: Portunoidea: Carcinidae), a nonindigenous species in Massachusetts, USA

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ABSTRACT

The population of the nonindigenous green crab *Carcinus maenas* (Linnaeus, 1758) in Salem Sound, Massachusetts, USA, was studied over a three-year period from July 2013 through June 2016 using baited traps deployed monthly at five sites. Seasonal catch per unit effort, sex, size, and color were determined and the role of habitat variables, including temperature, salinity, water depth, and substrate, were evaluated. Seasonal catch per unit effort was highest in the fall (October-December), followed by summer (July-September), spring (April-June) and winter (January-March). Few crabs were captured when water temperature dropped below 5 °C. Crabs captured at sites with very fine sand were larger than those captured on other sediment types. Females comprised 73% of the total catch of 7,822 crabs. Only 57 individuals exceeded 70 mm carapace width. Females were larger (mean = 51.7 mm) than males (mean = 48.8 mm). Green-phase crabs comprised 56.8% and red-phase crabs 43.2% of the catch. Green-phase crabs were significantly smaller (mean = 48.1 mm) than red-phase crabs (mean = 53.6 mm, $P < 0.0001$). Red-phase females were most common in the spring and green-phase in the fall, whereas red-phase males were most common in the spring and fall and green-phase in the summer. A yellow-phase category is proposed as a distinct intermediate between red and green phases. Merits of various types of traps and of bait were evaluated based on different trapping requirements and goals. This is the first investigation of multiple aspects of a population of *C. maenas* in Massachusetts. The findings should prove useful for researchers studying other populations of *C. maenas*, as well as for commercial crab fishers or others trapping green crabs for bait, or in efforts to reduce population numbers of this destructive invasive species.

Key Words: crab traps, crab bait, marine invasive species, marine nonindigenous species, population dynamics, seasonal catch per unit effort, sex ratio, ventral coloration

INTRODUCTION

The European green crab *Carcinus maenas* (Linnaeus, 1758) (Carcinidae MacLeay, 1838) is native to the northeastern Atlantic coastline from Norway to Mauritania (Crothers, 1968; Elner, 1980; Carlton & Cohen, 2003; Roman & Palumbi, 2004). This species was introduced to the mid-Atlantic United States in 1817, presumably carried in solid ballast or within fouling communities and shipworm holes on the outside of wooden ship hulls (Chilton, 1910; Almaça, 1963; Vermeij, 1982; Cohen *et al.*, 1995; Carlton & Cohen, 2003; Eastwood *et al.*, 2007; Darling *et al.*, 2008). They spread northward, arriving in northeastern Massachusetts, New Hampshire, and southern Maine waters in the 1890s or early 1900s, and eventually to Nova Scotia, Canada by the early 1950s and Prince Edward Island by 1997 (Smith, 1879; Rathbun, 1905, 1930; Glude, 1955; Grosholz & Ruiz, 1996; Behrens Yamada, 2001; Audet *et al.*, 2003; Carlton & Cohen, 2003). Individuals were found in Newfoundland in 2007 (Klassen & Locke, 2007), but it is likely that this population represents a subsequent invasion from northern Europe rather than a northward expansion of the crabs introduced in 1817 (Roman, 2006; Darling *et al.*, 2008; Blakeslee *et al.*, 2010; Darling, 2011; Blakeslee, 2013). *Carcinus maenas* was the most commonly encountered species of crab in the rocky and cobble intertidal areas along the New England coastline throughout at least the latter half of the 1900s (Grosholz & Ruiz, 1996; Lohrer & Whitlatch, 2002; Whitman, 2004; Tyrrell *et al.*, 2006). This range includes the region studied, Salem Sound, which is located along the northeast coast of Massachusetts. The recent introduction of another nonindigenous species, the Asian shore crab *Hemigrapsus sanguineus* (De Haan, 1835), along the western Atlantic coast in 1988 (Williams & McDermott, 1990; McDermott, 1998), and its arrival in Salem Sound in 1999 (Chase *et al.*, 2002) has greatly reduced the numbers of *C. maenas* in the rocky intertidal habitat of this area (Lohrer & Whitlatch, 2002; Griffen *et al.*, 2008; AMY, personal observation). *Hemigrapsus sanguineus* is often the most abundant crab in boulder and cobble intertidal shorelines from New England to Long Island, NY (Ahl & Moss, 1999; Gerard *et al.*, 1999; Casanova, 2001; Ledesma & O'Connor, 2001; O'Connor, 2001), but *C. maenas* is still the dominant species of crabs in estuaries with muddy or sandy bottoms.

Carcinus maenas is an opportunistic omnivore, known to consume an extensive variety of prey items, including organisms from at least 158 genera in five plant and protist and 14 animal phyla (Cohen *et al.*, 1995). Crabs become more carnivorous with age, with adults showing a strong preference for bivalve molluscs such as blue mussels *Mytilus edulis* Linnaeus, 1758, and soft-shell clams *Mya arenaria* Linnaeus, 1758 (Ropes, 1968). *Carcinus maenas* has caused considerable damage to beds of blue mussels (DeGraaf & Tyrrell, 2004), American oysters *Crassostrea virginica* (Gmelin, 1791) (Miron *et al.*, 2005), and eelgrass *Zostera marina* Linnaeus, 1758 (Davis *et al.*, 1998; Malyshev & Quijón, 2011; Garbary *et al.*, 2014; Neckles, 2015) along the New England coast. Perhaps most important from an economic standpoint, *C. maenas* has had a significant negative impact on the soft-shell clam industry in New England (Smith & Chin, 1951; Glude, 1955; MacPhail *et al.*, 1955; Ropes, 1968; Welch, 1968; Beal, 2002; Whitlow, 2010) because green crabs consume large quantities of clams. Some of the poorest clam harvest years in Massachusetts and Maine have followed high population levels of *C. maenas* and, conversely, some of the highest clam harvests have followed declines in the *C. maenas* population, which were probably due to environmental factors such as extremely cold winters (Glude, 1955; Welch, 1968; Elner, 1980). The early part of this decade has seen a large increase in the *C. maenas* population in Maine, New Hampshire, and northeastern Massachusetts, followed by a subsequent sharp decline in the commercial harvest of soft-shell clams in 2013 and 2014 (Atlantic Coastal Cooperative Statistics Program; http://www.accsp.org). Trapping crabs as a way to reduce the *C. maenas* population in areas of clam flats is of interest to the New England shellfish fishery. Factors including the best type of trap, best bait, and most favorable time of the year to trap are important considerations for clam fishers as well as crabbers who sell crabs as bait or for other uses.

The name "green crab" for *C. maenas* is somewhat of a misnomer because, although the dorsal surface is typically a mottled olive green to brownish green, the ventral surface may exhibit a range of colors, including green, yellow, orange, and red. Recent post-molt crabs are usually pale green (McGaw *et al.*, 1992; Wolf, 1998; Audet *et al.*, 2008), although some may be more yellow (Gillespie *et al.*, 2007) and some females remain red immediately after ecdysis (Kaiser *et al.*, 1990; Lee & Vespoli, 2015). During intermolt periods, or anecdysis, the ventral surface color transitions through yellow to orange to red (Cheung, 1966; Crothers, 1967; McGaw & Naylor, 1992a; Fulton *et al.*, 2013b; Lee & Vespoli, 2015). It is not known what causes these color changes but they may be due to photo-denaturation of the integument carotenoid pigments to reveal more red-colored astaxanthin or various carotenoprotein complexes (Lenel, 1953, 1955; Jencks & Buten, 1964; Lee, 1977; Garate *et al.*, 1984; Shahidi *et al.*, 1998; Styrishave *et al.*, 2004; Wade *et al.*, 2009). Another possibility is that the color changes are due to a thickening of the exoskeleton that normally masks the actions of three monochromatic red, white, and black chromatophores (Powell, 1962), thereby making the calcified salts and yellow and orange pigments in the outer layer of the exoskeleton more visible (Crothers, 1968). It is known that carotenoids, including astaxanthin, are beneficial in gonadal development and maturation, fertilization, hatching, viability, and growth (Shahidi *et al.*, 1998). Whatever the cause of the color changes, it is known that crabs in an extended intermolt get progressively reddish. *Carcinus maenas* may molt while yellow or orange or even red, but once a crab enters into a terminal anecdysis after about ten molts following the puberty molt (Carlisle, 1957), it almost always becomes red and often will acquire epibionts and shell necrosis on the dorsal carapace, both indicative of an aged shell. There is evidence that different colored *C. maenas* vary in behavior and physiology (Reid & Aldrich, 1989; Reid *et al.*, 1989; Kaiser *et al.*, 1990; McGaw & Naylor, 1992 b, c; Abelló *et al.*, 1994; Reid *et al.*, 1994, 1997). Red males are less tolerant to physiological stress, but are generally larger and presumably able to acquire more females for mating (Van Der Meeren, 1994). Post-molt adult females devote their energy resources to reproduction rather than growth and mating, resulting in their redder color. Individuals that devote their resources to growth, molt more frequently and are greener. Color distribution can therefore indicate whether a population is in reproductive or growth mode (Rewitz *et al.*, 2004; Lee & Vespoli, 2015). Due to the difficulty of quantifying what is actually a continuum of color, crabs often are simply divided into "green" or "red" phases but such approach does not consider the possibly distinct characteristics of intermediate yellow crabs. Fulton *et al.* (2013b) assigned Munsell color designations of value, chroma, and hue (Munsell Color Company, 1950) to each crab they examined but this results in different designations, each consisting of three numerical values. Lee *et al.* (2005) developed a simple color index that assigned numerical values of 1–10 for ten colors ranging from green to dark red. We used a slightly modified version with twelve colors.

Fulton *et al.* (2013a, b) examined distribution, sex, size, and color in populations of *C. maenas* in two New Hampshire estuaries, the first and only known study from New England. We report on a three-year trapping survey to determine seasonal catch, sex ratios, and ventral coloration of *C. maenas* in the Salem Sound estuary in northeastern Massachusetts. Trapping surveys do not determine the abundance of crabs in different months or seasons but rather the number of crabs captured based on foraging activity. The actual abundance could or could not change but increased or decreased feeding activity will result in higher or lower catches. Conclusions regarding attributes of the population of *C. maenas* in Salem Sound are based on the assumption that the actively feeding crabs that enter traps are a reasonable representation of the whole population (Rewitz *et al.*, 2004).

Information on the population dynamics of *C. maenas* is of importance to identify the best times during the course of the year to trap crabs for maximum effect with the least amount of effort. It would be most effective for eradication efforts to perform trapping when crabs are most actively foraging for food and therefore entering traps frequently. For potential use for human consumption, larger *C. maenas* are preferable to smaller crabs so it is useful to know the size distribution of crabs. For the consumption of soft-shell crabs, it would be necessary to know when and how many crabs could be expected to molt at particular times of the year, and because molting is tied to ventral coloration, knowledge of the distribution of color phases throughout the year would be useful. Because the most effective traps and bait are important considerations for any of these activities, several commercially available traps and commonly used baits were evaluated for effectiveness in catching *C. maenas*. Variation in catch at different water depths and on different substrates also was evaluated. This information should prove useful to those wishing to trap *C. maenas* for food or to use as fishing bait or to reduce population numbers of this destructive invasive species.

MATERIALS AND METHODS

Monthly trapping protocol

Salem Sound, Massachusetts is a 36.6 km^2, high-salinity (28–32‰) coastal embayment with a mean semi-diurnal tidal range of approximately 2.75 m. It borders and includes the estuarine river systems within the northeastern Massachusetts communities of Manchester-by-the-Sea, Beverly, Danvers, Peabody, Salem, and Marblehead. Monthly trapping of crabs within the Salem Sound estuary was undertaken from July 2013 to June 2016 at five sites chosen in the Salem, Beverly, and Danvers areas of Salem Sound representing different sections of the estuary: Hawthorne Cove Marina (HCM) located in inner Salem Harbor; Winter Island (WI) public landing in the outer Salem Harbor; Beverly Pier (BP) commercial dock near the mouth of the Danvers River as it enters Beverly Harbor; Hill's Yacht Yard (HYY) in Beverly on the Bass River near its entrance into the Danvers River; and Pope's Landing (PL) near the head of the Porter River in Danvers (Fig. 1, Table 1).

Rectangular "Ketcham" box traps (Table 2) were deployed off docks at the five sites between the ninth and eleventh days of each month. Trapping was terminated in November 2014 but was resumed in April 2015 to evaluate the effect of an exceptionally cold winter when water temperatures at the Cat Cove Marine Laboratory dock dropped to 1 °C in December 2014 and –1°C during February and early March 2015 (T. Maney, personal communication). Time of trap deployment and retrieval was recorded each time but no effort was made to set traps at the same time of the day. All different times of day and night were covered because traps were allowed to soak, or remain underwater, for 48 h.

Traps were baited with fish carcasses of various species, primarily swordfish and salmon, provided by local fish markets until September 2014, after which only frozen whole herring was used. After a 24 h soak, crabs were removed, traps re-baited and allowed to soak for an additional 24 h. Total soak time on the bottom was approximately 48 h. All *C. maenas* individuals captured were bagged and frozen for future analysis. Incidental by-catch was noted and released.

Temperature and salinity were measured using a YSI Model 30 salinometer (YSI, Yellow Springs, OH) at the time when traps were set.

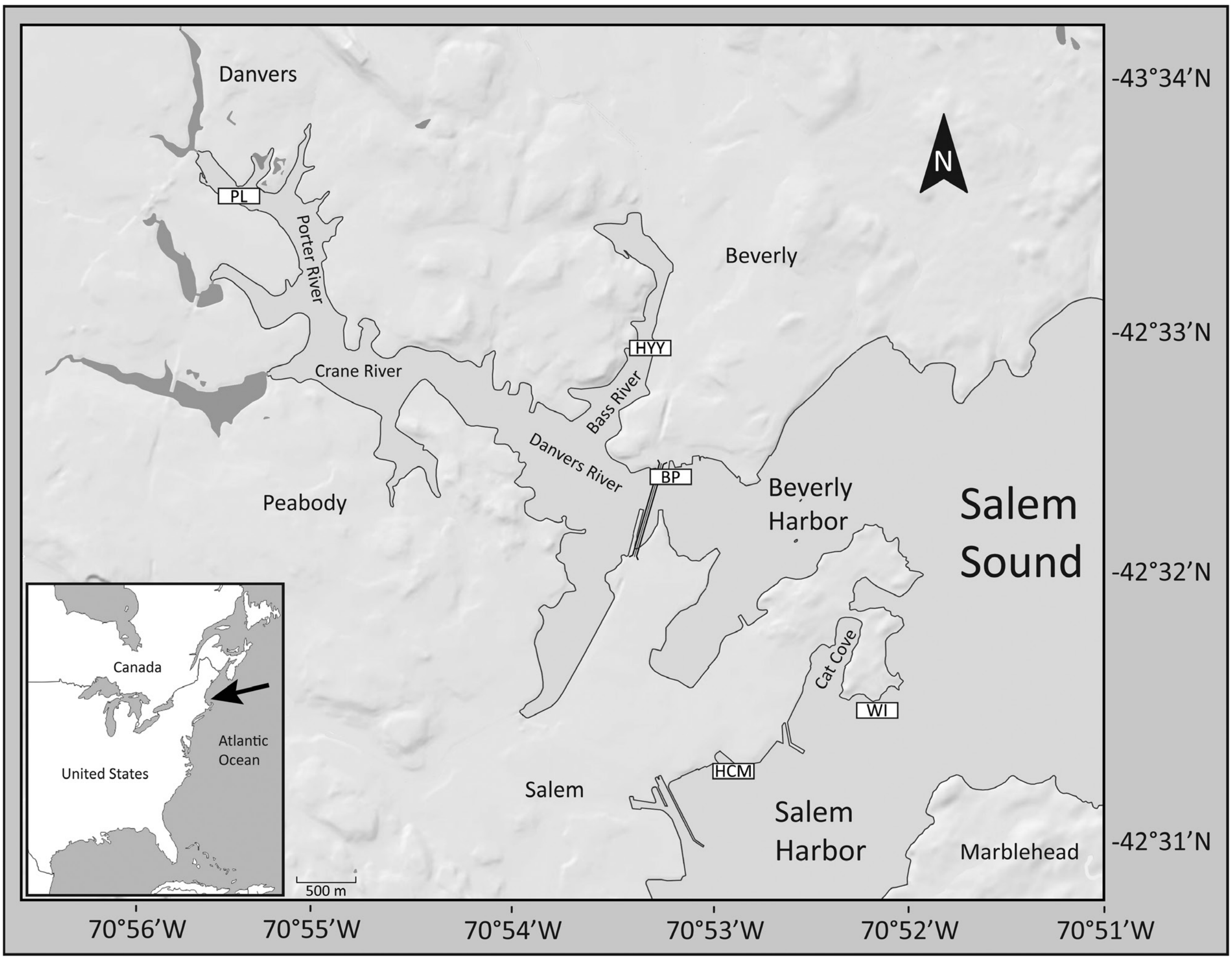

Figure 1. Locations of trapping sites for the green crab *Carcinus maenas*. HCM, Hawthorne Cove Marina (Salem Inner Harbor); WI, Winter Island (Salem Outer Harbor); BP, Beverly Pier (Danvers River/Beverly Harbor); HYY, Hill's Yacht Yard (Bass River, Beverly); PL, Pope's Landing (Porter River, Danvers). Inset shows location of Salem Sound (arrow) along the Massachusetts, USA, northeastern coast.

Table 1. Locations and physical characteristics of *Carcinus maenas* trapping sites in Massachusetts, USA.

Site	Location	Sediment				Temperature (°C)		Salinity (‰)	
		median grain size (mm)	kurtosis	skewness	Wentworth size class	mean	range	mean	range
HCM	42°31′15″N 70°52′54″W	0.90	– 0.3	0.8	coarse sand	11.5	1.8–20.5	31.0	27.2–32.5
WI	42°31′32″N 70°52′09″W	4.00	5.3	–2.3	pebble	11.4	1.9–19.8	30.9	23.5–32.6
BP	42°32′46″N 70°53′11″W	0.25	7.3	2.6	very fine sand	11.5	2.6–19.9	30.2	19.7–32.5
HYY	42°32′53″N 70°53′12″W	0.25	1.8	1.5	very fine sand	12.4	1.7–28.3	29.7	20.6–32.9
PL	42°32′25″N 70°55′20″W	0.50	0.8	1.0	medium sand	12.7	0.3–25.1	28.9	23.1–31.0

HCM, Hawthorne Cove Marina (Salem Inner Harbor); WI, Winter Island (Salem Outer Harbor); BP, Beverly Pier (Danvers River/Beverly Harbor); HYY, Hill's Yacht Yard (Bass River, Beverly); PL, Pope's Landing (Porter River, Danvers).

Table 2. Features of traps used to capture *Carcinus maenas* in the trap-comparison trial. Volume is space available for crabs after deducting entry designs, but does not account for space occupied by a bait bag. Weight includes any built-in concrete ballast; D, diameter; H, height; L, length; VCW, vinyl coated wire; W, width.

Trap	Material mesh (mm)	Entry type (number of entries)	Entry opening (mm)	Dimensions (cm)	Volume (cm^3)	Weight (kg)	Access
"Ketcham"	VCW 13 × 25	top PVC pipe (1)	76 D	46 W × 60 L × 23 H	63,000	4.5	top flap
"Terminator"	VCW 13 × 25	top slots (2)	76 W × 127 L	60 W × 60 L × 38 H	136,800	7.3	top flap
"slanted-sides"	VCW 13 × 25	sides (2)	38 W × 600 L	60 W × 60 L × 41 H	40,600	6.8	top flap
"trapezoidal"	VCW 13 × 25	top slot (1)	76 W × 127 L	46 bottom, 28 top × 90 L × 25 H	83,300	8.6	end flap
"Blanchard"	VCW 13 × 25	inverted cone ends (2)	38 W × 114 L	46 D × 90 L	129,500	12.7	removable end
eel	VCW 13 × 25	end chute (1)	63 W × 63 H × 580 L	30 W × 89 L × 30 H	77,800	7.3	end flap
minnow	galvanize steel wire d 6 × 6	inverted cone ends (2)	enlarged to 50 D	18 D × 40 L	9,700	0.5	separates in half

"Ketcham" is a modified Cuttyhunk Island (Massachusetts)-style box trap designed, manufactured and sold by Ketcham Traps Company, New Bedford, MA, USA. "Terminator" (based on a design by Russell Nickerson, Port Mouton, Nova Scotia, Canada), "slanted-sides," "trapezoidal," and eel box traps are manufactured by Brooks Trap Mill, Thomaston, ME, USA, and sold by Three Lantern Marine, Gloucester, MA, USA. "Blanchard" trap is a cylindrical trap designed, manufactured and sold by Andy Blanchard, Scarborough, ME, USA. Minnow traps are widely available at sporting goods stores. Eel and minnow traps are designed to catch fish, not crabs, but both can be used.

Assessment of trap escapement

To evaluate potential escapement of crabs from "Ketcham" traps used in the survey, 25 crabs were placed in an un-baited trap and left to soak for 5 days. In a second test, an un-baited trap with 25 crabs was placed in a large holding tank with running seawater, and fish bait was positioned around the outside of the trap as inducement for escape.

Comparisons of tide and time of day

The closest high or low tide was noted at the time of trap deployment but no effort was made to synchronize trap deployment with tides. A trial was conducted to evaluate the effect of time of day and tide phase on catch of *C. maenas*. During June 2015, a trap was baited and set at the time of a noon high tide and was hauled every 3 h for 24 h. The protocol was repeated a week later, beginning at a noon low tide. Crabs captured were counted to determine catch per unit effort per trap (for 3 h) and sex, but not color, was determined for all crabs collected during the trial.

CPUE, size, color and sex of Carcinus maenas

Mean 48 h extrapolated catch per unit effort was calculated for each sample site per month and season. All crabs were sexed and carapace width (CW) (tip to tip of fifth spines) was measured to the nearest 0.1 mm with calipers (Model 31-415-3, Swiss Precision Instruments, Garden Grove, CA). Because crabs < 25 mm CW easily escaped through the trap mesh, very few small individuals were captured and are under-represented in the catch, and were not included in statistical analyses or in calculations of reported mean CW so as not to over-estimate the average size within the total population.

A color index (CI; modified after Lee *et al.*, 2005) consisting of twelve numbered color chips cut from paint-color swatches (Fig. 2) was used to determine ventral coloration based on the color of the third maxillipeds, which was less variable among individuals than the sternites or abdomen (Fig. 3). Colors associated with CI values are as follows: 1, dark green; 2, light green; 3, yellow-green; 4, greenish yellow; 5, light yellow; 6, dark yellow; 7, yellow-orange; 8, light orange; 9, dark orange; 10, orange-red; 11, red; 12, dark red. Each crab was assigned either a whole number value or a half-value (whole number plus 0.5) if it fell between two color chips. Crabs having an odd combination of colors (e.g., orange green) were assigned the index value of the more dominant color. Fewer than 1% of crabs were brown or white or otherwise did not match any color and were not assigned a CI value or included in subsequent ventral color analysis. To simplify data analysis, the 23 CI values (1, 1.5, 2, 2.5 … 12) assigned to crabs were combined into five separate color groups: green (1.0–2.5), yellow-green (3.0–4.5), yellow (5.0–6.0), orange (6.5–9.0), and red (9.5–12.0). Carapace width and color of gravid females were noted.

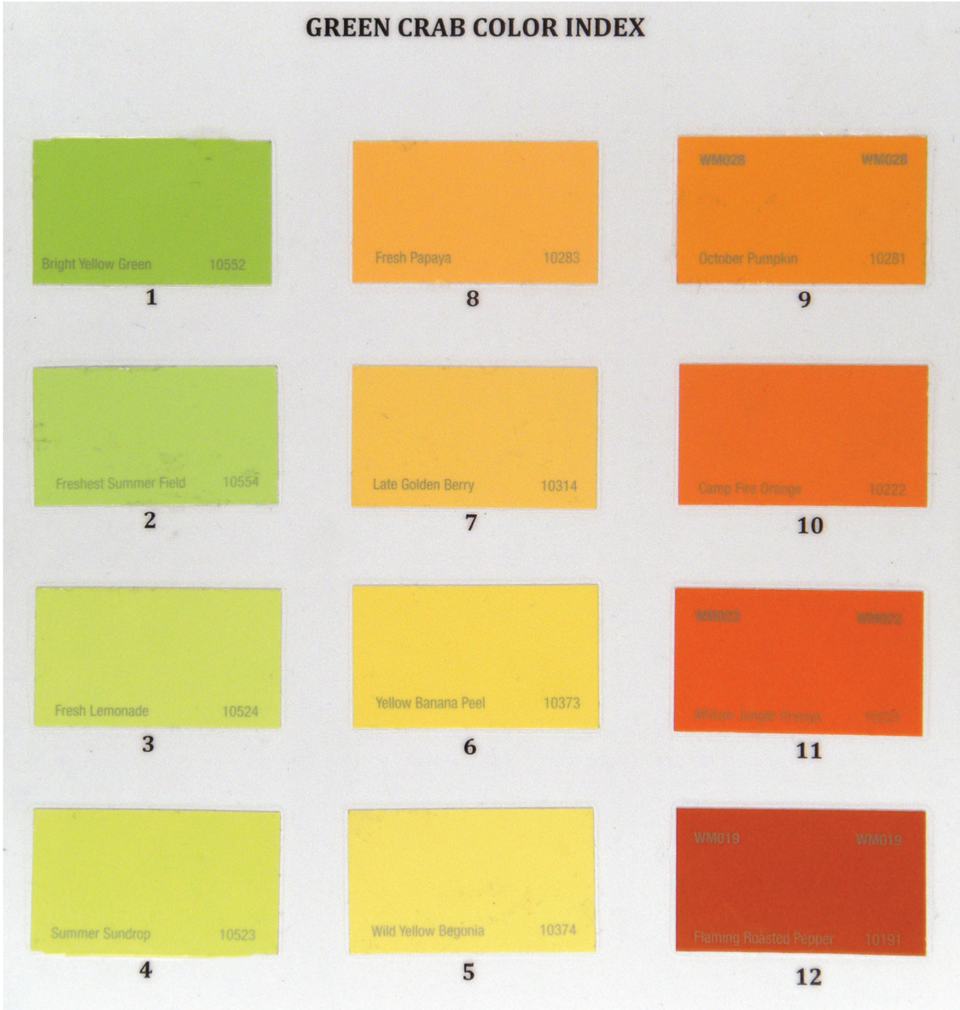

Figure 2. Color index used to quantify ventral coloration in *Carcinus maenas*. Color chips are sections of paint swatches. Color of third maxillipeds was matched to a color chip to determine the appropriate color index (CI) value.

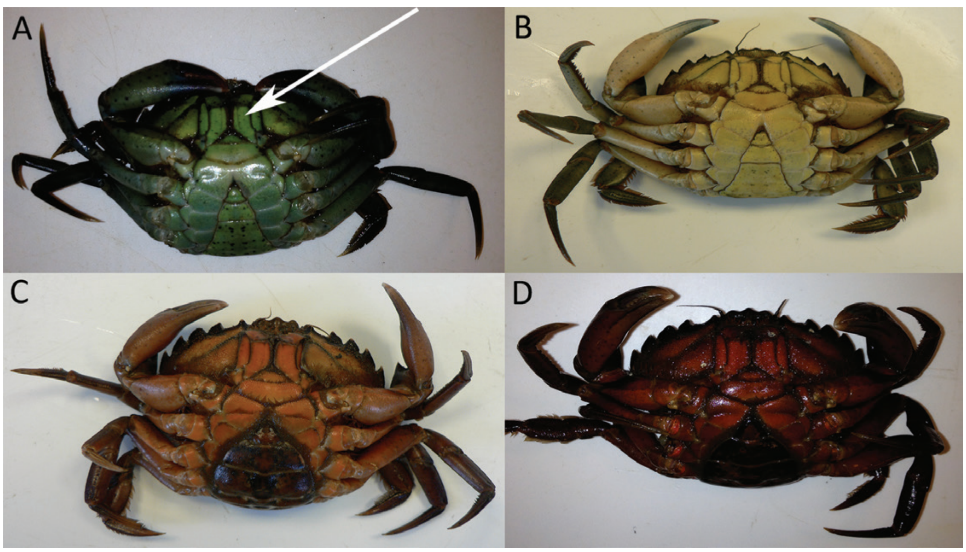

Figure 3. Examples of *Carcinus maenas* ventral coloration. Arrow points to third maxillipeds that were used to determine color index (CI) values. A, green male (CI = 1); B, yellow male (CI = 6); C, orange female (CI = 9); D, red female (CI = 12).

Substrate characteristics

A sample of the top 10–15 cm of sediment was collected from each trapping site and sorted wet through a series of 20.3 cm (8 in) Tyler sieves ranging from 8 mm to 0.063 mm (–3, –2, –1, 0, 1, 2, 3, 4 ϕ). Fractions were dried at 100 °C for 48 h and weighed. Size fraction percentages were used to determine values of kurtosis (peakedness) and skewness and to plot size distribution curves. A designation of Wentworth size class (Wentworth, 1922) for each site was based on mean grain size calculated as the average of Q_{18}, Q_{50} (median) and Q_{84} percentiles that were determined graphically from the distribution curves. The catch of crabs per unit effort at each trapping site was evaluated relative to substrate type.

Comparison of traps

Various trap designs were compared for effectiveness in catching *C. maenas*. Catch efficiency of several commercially available crab traps (Table 1, Fig. 2) was compared at Cat Cove Marine Laboratory dock at Smith Pool in Salem Harbor (42°31′4′′N, 70°52′18′′W) in September 2014 and June 2016 and at the Beverly Pier (BP) monthly trapping site in July 2015. In addition to the "Ketcham" box traps used throughout most of the study, six other traps were tested for catch efficiency. Traps included the "Terminator" and "slanted-sides" box traps, a "trapezoidal" trap, a cylindrical-design "Blanchard" trap, and two additional traps not specifically designed for crabs but often used to catch *C. maenas*: an eel trap and a small minnow trap (Table 2, Fig. 4). Each trap was baited with herring and deployed off a dock with at least 2 m separation between traps. Salinity and temperature were measured at the time of trapping. After a 24 h soak, crabs were removed, traps were re-baited, and rearranged along the dock area to eliminate possible differences due to trap location, and allowed to soak for an additional 24 h. Sex, CW, and ventral coloration CI values were determined for each individual and mean 48 h catch per unit effort per trap was calculated for each trap type.

Comparisons of bait

The types of bait were compared for catch effectiveness in May 2014 and October 2015 at the BP trapping site, and in September 2014, June 2015, and June 2016 at the Cat Cove Marine Laboratory dock. For each of the five bait trials, six traps were baited with different baits placed in hanging bait bags and allowed to soak for up to 24 h, after which time crabs were removed, traps were re-baited, rearranged along the dock to eliminate possible differences due to trap location, and allowed to soak for an additional comparable time. Due to varying availability of different baits during the several bait comparison trials, some of the five different baits compared were used more often than others, ranging from five times for herring, halibut, swordfish, and salmon to three times for tilapia, and twice for sardines. Sex, CW, and ventral coloration CI values were determined for each crab and mean 48 h catch per unit effort per trap was calculated for each bait type.

Comparison of water depth

Depth *versus* total catch was evaluated in September 2014 and October 2014 by setting identical "Ketcham" box traps baited with herring at depths of 1.5, 3.0, 4.5, and 6.0 m off docks at Beverly Port Marina (42°32′25′′N, 70°53′4′′W). After a soak of 24 h, crabs were removed, and traps were re-baited and allowed to soak for an additional 24 h. Single traps were set in October 2014 at depths of 8.5 m and 10 m at a location (42°3′13′′N, 70°52′27′′W) in a channel in Salem Harbor outside the survey study area. Sex and CW were determined for all crabs, and mean

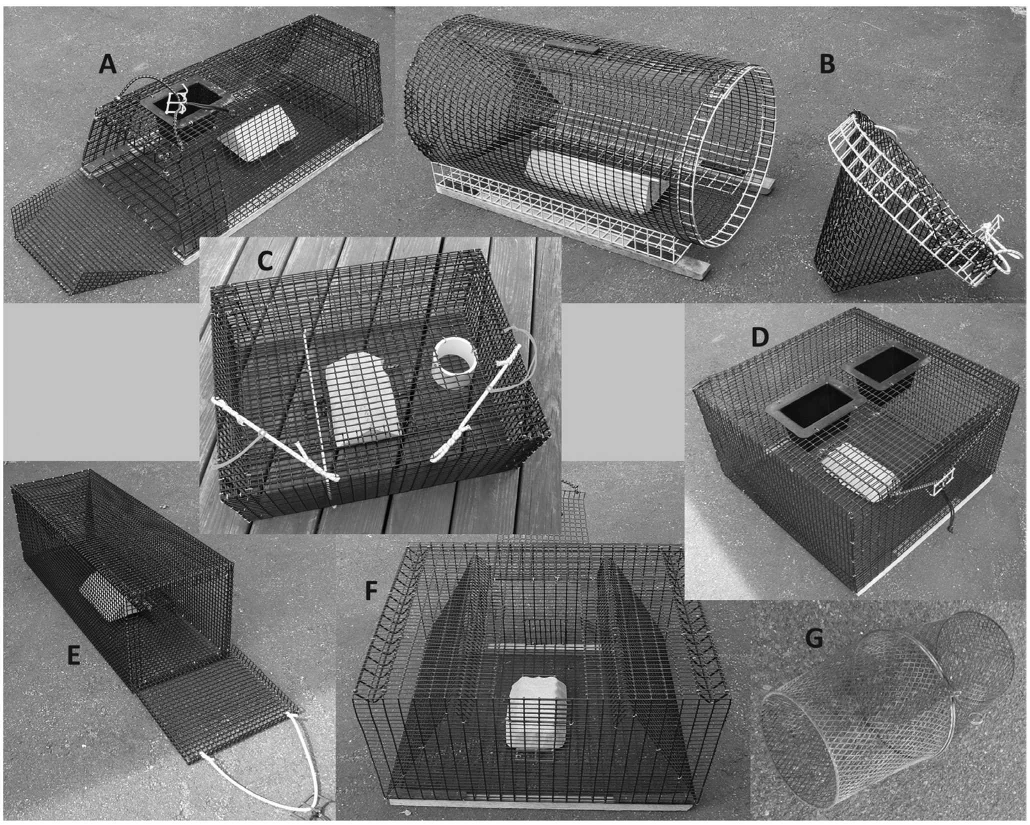

Figure 4. Common commercially available traps compared for ability to capture green crabs *Carcinus maenas*. A, "trapezoidal" trap; B, "Blanchard" cylindrical trap; C, "Ketcham" box trap used in the monthly survey; D, "Terminator" box trap; E, eel trap; F, "slanted-sides" box trap; G, minnow trap.

catch per unit effort (48 h) was calculated for each depth between 1.5 and 6.0 m. Catch data from the 8.5 and 10 m depths were excluded from statistical comparisons because only a single trap was set on one occasion at each of those two depths at a location some distance from the trapping study area in a channel with stronger tidal currents than at any of the survey trapping sites.

Analysis of data

A Mann-Whitney-Wilcoxon test (hereafter referred to as Wilcoxon test) and Kruskal-Wallis ANOVA (if there were more than two levels being compared) were used for each pair in which non-normal distribution was ranked for several sample groups. Where ranks were indicated under the Wilcoxon test, the test was performed individually for each pair. A Student's t-test was used for several analyses where normality assumptions were met and/or parametric and non-parametric results were equal. Spearman's ρ non-parametric regression was used to test the relationship between temperature and catch per unit effort, and between temperature and CW. Temperature and salinity for the trapping sites were ranked using Tukey's honestly significant difference (HSD) post hoc test, which provided a conservative alpha-level for the large data sets.

For all the monthly sampling data, a Kolmogorov Smirnov two-sample test was used to evaluate the statistical difference in CW distribution between male and female crabs captured. A Median test was used due to the presence of outliers in some of the data because such outliers could yield errors in variance if central tendency is used for analysis, thus misrepresenting the non-parametric data. Significance of variation in catch per unit effort by season and year was evaluated using a Kruskal-Wallis ANOVA followed by Dunn's non-parametric significance test of stepwise comparison or the Wilcoxon test for each pair, depending upon the size of the data set. Even though the crab-color data are presented as categorical, an exception was made in this instance, as a larger color-group value number always indicated more red color, whereas a lower value number always indicated a greener color. It was therefore possible to compare not only the variance between color and CW using a Wilcoxon test by creating grouped categories, but also the relationship via a non-parametric regression analysis. To test variation in crab size for different sized traps in the independent trap preference trial, a Wilcoxon rank test was used to test the relationship between ventral color and CW. A Median test was used to test variance in catch per unit effort among the different traps and a Wilcoxon test was used to generate an ordered difference report. In the studies where crabs were captured at several different depths, and in the bait comparison trial, a one-way ANOVA was used prior to a Student's t-test. All the statistical tests were performed using JMP Statistical Software Version 13.0 (SAS Institute, Inc., http://www.jmp.com).

RESULTS

Physical characteristics of trapping sites

Throughout the course of the 3-year monthly survey, the average temperature for all sites ranged from 0.6 to 21.9 °C, with the lowest temperature reading (0.3 °C) recorded at PL in January 2014 and the highest (28.3 °C) at HYY in July 2013. When temperatures for all sites were averaged for each month over the 3-year period, the warmest temperatures occurred in July (average = 20.9 °C), and the coldest in February (average = 2.9 °C). For each season, the mean water temperature for all trapping sites combined was 11.8 °C (spring), 19.0 °C (summer), 10.3 °C (fall), and 5.0 °C (winter), all significantly different from each other ($P < 0.0001$).

The average salinity at all sites was 29.9‰, with a range of 25.0 to 31.6‰. Fall and winter average salinities for all sites combined were significantly higher in fall (30.7‰) and winter (30.8‰) than during the spring (29.1‰) and summer (29.5‰) ($P < 0.05$).

Bottom sediments at four of the five sites, (HCM, BP, HYY, and PL) could be described as soft black mud with scattered mussel shells while the fifth site, WI, consisted of sandy mud and shell hash. Based on grain size analysis of the sediments (Table 2) the BP and HYY bottom can be categorized as Wentworth Size Class "very fine sand". Size distribution curves for both sites show considerable peakedness with positive skewness toward fine grain size. The PL site can be categorized as "medium sand" and exhibits a distribution curve that is close to normal with positive skewness toward finer grains. The mean grain size at the HCM site indicated "coarse sand," with the distribution curve showing no peakedness and positive skewness toward fine grains. The WI site was the most different from the other four sites, categorized as "pebble" and a size distribution curve showing considerable peakedness and negative skewness toward coarse grains.

Assessment of trap escapement

Results of both "Ketcham" trap escapement tests showed that none of the crabs in the trap were able to escape, even when bait was offered outside the trap as inducement. Escape would only be possible if the trap became filled with crabs to the point when they could reach and crawl out of the entry slots, a condition that never occurred during the course of our study. We are thus confident that all crabs that entered a trap were retained and catch per unit effort values are reflective of the actual number of crabs captured per soak.

CPUE, size, color, and sex of Carcinus maenas

Average total catch per unit effort (CPUE) and temperature for all sites combined per season is shown in Figure 5. Median (used instead of mean due to the large variation among samples) CPUE was 7 during spring (April-June), 19 during the summer (July-September), 38 during the fall (October-December), and one during the winter (January-March). Catches were not statistically different from each other, although fall catches were significantly different from both spring and winter catches ($P < 0.0001$). Average CPUE per month was significantly higher in 2015 mean = 85) and 2016 (mean = 84) than in 2014 (mean = 26) ($P < 0.05$), and 2014 CPUE was significantly higher than in 2013 (mean = 41) ($P < 0.001$). There was no significant difference in average CPUE in 2013 compared to 2014, 2015, and 2016. Temperature had a weak to moderate positive correlation with CPUE ($\rho = 0.216$, $P < 0.01$). There was no significant difference in mean total CPUE before and after September 2014, when bait was altered from mixed fish to only herring. Despite the variation in salinity among sites, there was no correlation between CPUE and salinity.

Females comprised approximately 73% of the total catch (7,822) captured during the monthly trapping survey and, on average, females were larger than males (Table 3). Although females comprised the majority of the overall catch, the sex ratio varied with season. The average proportion of females captured in the spring (mean = 61%) was significantly less than in summer (mean = 75%), fall (mean = 78%), and winter (mean = 69%) ($P < 0.05$). Overall, more females than males were captured at every site except PL, where 55% of all captured crabs were males.

When the ventral coloration CI values of *C. maenas* were reduced to five color groups, the green group comprised 13.2% of the crabs, yellow-green 20.4%, yellow 22.8%, orange 30.9%, and red 12.7% (Table 3). Color groups were further reduced to two major categories. Any crabs with CI values of 1.0–6.0 (indicating no red pigment) were classified under the green phase; crabs with some red pigment (CI values 6.5–12.0) under the red phase. Of all crabs captured, 55.5% belonged to the green phase and 44.5% to the red phase. Red-phase crabs were more common in spring, whereas green-phase crabs were more common in the remaining seasons. A higher proportion of red-phase males were captured in the spring and fall than in summer and winter, whereas the

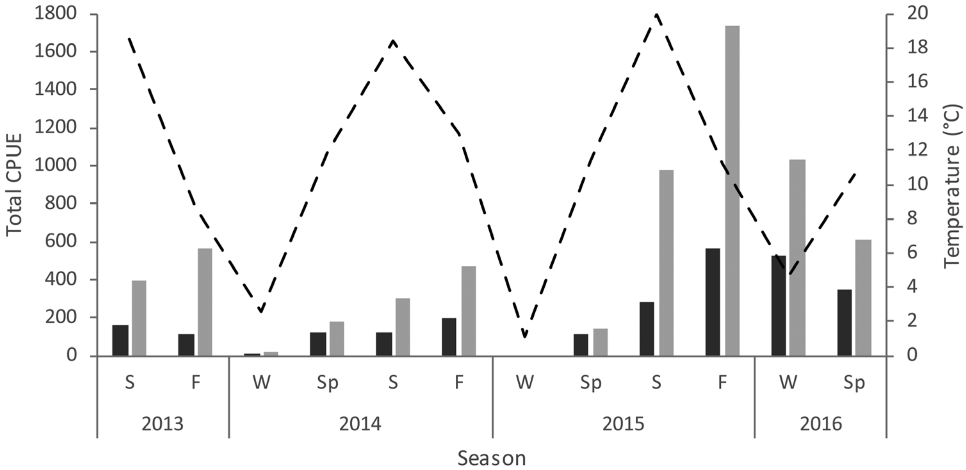

Figure 5. Seasonal *Carcinus maenas* 48-hour catch per unit effort (CPUE) per trap for all five trapping sites combined. Black columns represent males; grey columns represent females. Dashed line shows average temperature (°C) at sites. S (summer: July, August, September); F (fall: October, November, December); W (winter: January, February, March); Sp (spring: April, May, June). No trapping was conducted in December 2014, or January, February, and March (W) 2015.

Table 3. Numbers and sizes of male and female *Carcinus maenas* for each color group. Not included are brown or white individuals.

Color-index values	Color group*	Total number of crabs (%)	CW (mm) Mean (range) Total	Males	Females
1.0–2.5	G	1,025 (13.2)	40.3 (1.4–69.6)	35.6 (1.4–69.6)	42.6 (2.0–66.5)
3.0–4.5	YG	1,584 (20.4)	47.3 (3.0–80.5)	45.8 (3.0–80.5)	48.2 (13.3–73.8)
5.0–6.0	Y	1,769 (26.8)	53.4 (18.7–81.9)	52.7 (18.7–77.1)	53.7 (26.7–81.9)
6.5–9.0	O	2,394 (26.9)	53.1 (14.8–85.9)	55.5 (14.8–76.0)	52.5 (8.4–85.9)
9.5–12.0	R	981 (12.7)	54.7 (42.6–70.0)	57.6 (42.6–70.0)	54.5 (30.1–69.7)
1.0–6.0	GP	4,378 (56.5)	48.1 (1.4–81.9)	46.2 (1.4–80.5)	49.1 (2.0–81.9)
6.5–12.0	RP	3,375 (43.5)	53.6 (14.8–85.9)	55.7 (14.8–76.0)	53.2 (18.4–85.9)
1.0–12.0	all	7,753 (100)	50.5 (1.4–85.9)	48.8 (1.4–80.5)	51.2 (2.0–85.9)

*G, green; YG, yellow-green; Y, yellow; O, orange; R, red; GP, green phase; RP, red phase

highest proportion of red-phase females were captured in summer. Green-phase females were most abundant in the fall, whereas green-phase males were most abundant in summer (Table 4). The mean CI value varied at different trapping sites. The average CI value of crabs captured at WI with pebble sediment was significantly greater (redder) than that for crabs captured on any of the other sediment types, BP and HYY with very fine sand, PL with medium-size sand and HCM with coarse sand (Table 5). The average CI values for crabs captured on sites with pebble and very fine sand sediment were significantly greater than those of crabs captured at both medium-size and coarse sand sites ($P < 0.001$).

Of the captured crabs, 12.0% carried epibionts, primarily northern rock barnacles (*Semibalanus balanoides* (Linnaeus, 1767)) and slipper shells, (*Crepidula fornicata* (Linnaeus, 1758)). Of the fouled crabs, 84.4% had some red pigmentation, being classified as either orange or red, whereas 6.2% were green or yellow-green. Only 15 gravid females were captured; 13 (87%) were red-phase crabs and two had a yellow ventral coloration. The average CW of this very small sample of gravid crabs was 50.7 mm (31.9–65.5 mm). Seven of the 15 crabs were captured in the month of July (6 in 2013, 1 in 2014), 3 in August (2 in 2013, 1 in 2015), 2 in November 2013, 2 in May 2014, and 1 in January 2016.

The mean CW for all crabs (not including individuals < 25 mm) was 51.3 mm, with females (51.5 mm, $N = 5{,}654$) being significantly larger than males (50.6 mm, $N = 1{,}986$; $P < 0.0001$) (Table 5). The largest individuals were an 80.9 mm male and an 85.9 mm female. Few crabs (28 males and 29 females) were larger than 70 mm and only eight males and three females larger than

Table 4. Number of individuals (%) of *Carcinus maenas* in green (GP) or red (RP) phases.

	Spring	Summer	Fall	Winter
Total				
GP	542 (42.8)	1388 (54.7)	1,969 (64.5)	479 (53.6)
RP	725 (57.2)	1152 (45.4)	1,083 (35.5)	415 (46.4)
Males				
GP	296 (59.4)	557 (87.4)	459 (66.9)	199 (72.9)
RP	202 (40.6)	80 (12.6)	227 (33.1)	74 (27.1)
Females				
GP	246 (32.0)	831 (43.7)	1,510 (63.8)	280 (45.1)
RP	523 (68.0)	1072 (56.3)	856 (36.2)	341 (54.9)

spring (April-June, 2014, 2015, 2016); summer (July-September, 2013, 2014, 2015); fall (October-December, 2013, 2014, 2015); winter (January-March, 2014, 2016)

75 mm were captured. The average CW of red-phase *C. maenas* was significantly larger than that of green-phase crabs (53.6 *versus* 49.3 mm) ($P < 0.0001$). There was a difference in size among crabs captured during the four seasons, with mean CW of 52.8 mm (spring), 50.5 mm (summer), 51.1 mm (fall), and 51.7 mm (winter). The differences between summer, fall, and winter sizes were not significant but spring crabs were significantly larger than crabs captured in other months (Wilcoxon test, $P < 0.01$). Of the five color groups, mean CW was larger in the red crabs than in both the yellow and orange crabs. Average CW of yellow and orange crabs were not statistically different from each other, but both showed a significant difference compared to that of yellow-green crabs ($P < 0.05$). The green group exhibited the lowest average CW, which was significantly different from all four other color groups ($P < 0.05$). A total of 528 green-phase and 666 red-phase crabs were larger than 60 mm CW, whereas only 276 green-phase and 5 red-phase crabs had a CW < 30 mm.

Crabs captured at sites with very fine sand (BP and HYY) were significantly larger than crabs captured at sites with other sediment types (Table 4). Although a comparison of the average size of crabs captured in medium-size sand at PL and those captured in the pebble sediment at WI showed no statistical difference, crabs captured at both of these sites were significantly larger than those captured in the coarse sand at HCM ($P < 0.001$).

Comparisons of traps

There was a significant amount of variation in catch among the different trap types evaluated ($P < 0.05$; Table 6). Based on averages calculated from the three trapping trials, the large cylindrical “Blanchard” trap captured significantly more crabs than any of the other traps, except for the “trapezoidal trap” ($P < 0.001$). There was no significant difference between the “Terminator,” “slanted-sides,” and eel traps, but each captured fewer crabs than either the “trapezoidal” or “Blanchard” trap ($P < 0.01$). There was no statistically significant difference between the “Ketcham” and minnow traps, but both captured fewer crabs than the other four evaluated traps ($P < 0.05$). The small capacity of a minnow trap results in rapid saturation, thereby allowing crabs to escape and reducing further entry of crabs due to intimidation, as reported by Miller (1979). A smaller CPUE for the minnow trap was thus expected. No difference in the CI level was observed between crabs captured in different traps. Larger crabs tended to contain more red pigment than smaller crabs. The mean CW of green-phase crabs (39.2 mm) was significantly different than that of red-phase crabs (48.5 mm, $P < 0.001$). These results are similar to the monthly trapping data.

Mean CW of crabs was greatest for those captured in the “trapezoidal” trap, followed by the “Blanchard,” “slanted-sides,” “Terminator,” “Ketcham,” eel, and minnow traps (Table 7). Although crabs captured in the “Terminator” trap were smaller when compared to the “trapezoidal” trap, no difference in average CW was seen between the “Terminator” and “Blanchard” traps. The minnow trap, the smallest trap with a smaller mesh than the other traps, captured smaller crabs on average only when compared to the “Blanchard” (the largest) and the “trapezoidal” traps ($P < 0.01$).

Comparisons of baits

Of the baits compared, the highest CPUE was found with herring, followed by halibut, tilapia, swordfish, salmon, and sardines (Table 6). Significantly more crabs were captured with herring than with swordfish, salmon, or sardines ($P < 0.05$), but the number of crabs captured with halibut or tilapia showed no statistically significant difference when compared to catches with the other four baits. No apparent differences were observed in size, color, and sex ratios in the bait comparison trials compared to the much larger monthly trapping trial.

Comparisons of depths

There were no statistically significant differences between average CPUE per depth from the two depth comparison trials combined (Table 6). The mean CW for crabs captured at a depth of 1.5 m (53.6 mm) was not significantly different than the CW of crabs captured at depths of 3.0 m (53.7 mm), 4.5 m (52.6 mm), or 6.0 m (53.9 mm). A single female individual (CW 60.6 mm, CI 5) was captured in one of the two traps set at depths greater than 6 m, but this crab was not included in any statistical analyses.

Comparisons of tide stage and time of the day

During the small tidal stage/time of day trial, there was no significant difference in mean 3 h CPUE between the ebb tide (10 ± 2)

Table 5. Average size and color of *Carcinus maenas* caught at different trapping sites in Massachusetts. Mean CW does not include individuals < 25 mm. Mean color index values were rounded to nearest whole or half. HCM, Hawthorne Cove Marina (Salem Inner Harbor); WI, Winter Island (Salem Outer Harbor); BP, Beverly Pier (Danvers River/Beverly Harbor); HYY, Hill's Yacht Yard (Bass River, Beverly); PL, Pope's Landing (Porter River, Danvers).

Trapping site	Mean CW (mm) ± 1 SE	Mean color index
HCM	46.9 ± 0.4	5.0
WI	50.1 ± 0.4	6.5
BP	52.6 ± 0.1	6.5
HYY	51.3 ± 0.2	5.5
PL	49.9 ± 0.4	5.0

Table 6. Individuals of *Carcinus maenas* captured (mean 48 h catch per unit effort (CPUE) ± 1 SE) in separate set of trials involving comparisons of different types of traps, types of bait, and depths.

Trap trials		Bait trials		Depth trials	
Trap	CPUE	Bait	CPUE	Depth (m)	CPUE
“Blanchard”	501 ± 151	herring	394 ± 140	1.5	38 ± 15
“Terminator”	309 ± 110	halibut	191 ± 66	3.0	73 ± 29
“slanted-sides”	199 ± 98	tilapia	158 ± 101	4.5	36 ± 6
“Ketcham”	146 ± 46	swordfish	99 ± 38	6.0	51 ± 25
“trapezoidal”	272 ± 105	salmon	86 ± 22		
eel	228 ± 92	sardines	58 ± 30		
minnow	103 ± 27				

Frozen herring purchased from a local bait shop; halibut, swordfish, and salmon carcasses provided by local fish markets; tilapia provided by the Salem State University Cat Cove Marine Laboratory, Salem, Massachusetts; canned sardines purchased from a local grocery store..

Table 7. Average size of individuals of *Carcinus maenas* captured in different traps. Mean CW does not include individuals < 25 mm.

Trap	Mean CW (mm) ± 1 SE
“Blanchard”	43.6 ± 0.9
“Terminator”	39.4 ± 2.1
“slanted-sides”	39.8 ± 2.0
“trapezoidal”	47.1 ± 2.0
“Ketcham”	39.1 ± 1.0
eel	39.1 ± 1.7
minnow	38.4 ± 0.9

and the flood tide (4 ± 2). The time of day data were broken into daytime (0700 to 1900) and nighttime (1900 to 0700); there was no significant difference in mean 3 h CPUE between daytime (8 ± 2) and nighttime (5 ± 2). Neither the tide stage or time of day resulted in a significant difference in the sex ratio of captured crabs.

DISCUSSION

Results of trapping surveys such as this one are based only on actively feeding crabs that enter traps. Novak (2004) examined 22 studies of diel activity in *C. maenas*. Most reported higher activity levels during the night, but Hunter & Naylor (1993) and Grosholz *et al*. (2000) found no difference in diel *versus* diurnal activity level. In contrast, Novak (2004) found that *C. maenas* in the shallow subtidal of the Isles of Shoals, Gulf of Maine, USA (approximately 50–60 km north of our study site) were more active during the day than at night. Traps in the present study were soaked for 48 h, therefore covering both night and day periods. Bait was replenished after 24 h to prevent bias of fresh bait attracting more crabs than bait that had been in the traps for a period of time. There was no apparent difference in the number of crabs captured in the first 24 h period *versus* the second 24 h, regardless of whether traps were set in the morning or evening. Miller (1979) found that reduced entry and escapement from traps increased for species of *Cancer* when traps became saturated with crabs. Removal of *C. maenas* after 24 h eliminated the possibility of escapement and of reduced catch due to intimidation of later arrivals as a result of trap saturation. Crabs are not able to escape "Ketcham" traps as long as the trap is not filled with crabs to the point where those on top can reach the entry slot, and that was never allowed to happen. The change of bait in September 2014 apparently had no effect on the seasonal catch per unit effort (CPUE) because there was no significant difference between total overall CPUE before and after the bait shift. CPUE was greatest in the fall when the water was cooling but before the temperature dropped below ~5 °C, presumably due to increased foraging prior to winter quiescence (Styrishave & Andersen, 2000). As the water warmed in the spring to above ~5 °C, catch began to increase and continued into the summer. Feeding activity is known to increase prior to periods of molting although feeding ceases immediately before and after ecdysis (Ropes, 1968). Actively mating *C. maenas* have been found to have empty stomachs suggesting that they do not feed while sexually active (Ropes, 1968). An increase in feeding activity is also linked to periods of reproduction, when more food is needed for gamete production. This suggests that foraging prior to active mating increases for gamete production and to gain energy in preparation for fasting during mating. In addition, based on stomach contents, recently molted nearly hard-shelled *C. maenas* have shown greater appetites in comparison to hard-shelled crabs (Ropes, 1968). Crab foraging activity, and as a result, catch, increases in the early spring when crabs are recovering from a winter fast (Styrishave & Andersen, 2000) in preparation for molting and mating and again in the fall prior to overwintering when low temperature makes foraging impossible.

More female (73%) than male *C. maenas* were captured during the course of this survey. Studies in Europe (e.g., Broekhuysen, 1936; Aagaard, *et al*., 1995; Mathieson & Berry, 1997; Rewitz *et al*., 2004), Canada (Gillespie *et al*., 2007), and New England (McKnight *et al*., 2000; Fulton *et al*., 2013a; J. Grundstrom *et al*., unpublished data), have shown that skewed sex ratios favor females in waters with a higher salinity. For example, Rewitz *et al*. (2004) captured more females than males in the high-salinity Looe Estuary in England. High salinity is found throughout the Salem Sound estuary because the amount of freshwater input has been reduced due to intense development. Extensive impervious surfaces in the watershed channel rain and snowmelt into the local sewer system rather than allowing it to flow into rivers emptying into Salem Sound. Trapping site Pope's Landing (PL), the farthest from the harbors, had a somewhat lower average salinity than the other four trapping sites and it is the only location that saw a higher proportion of male (55%) than female *C. maenas*. Several studies suggest that female *C. maenas* are less tolerant of low salinity than males, evidenced by the tendency of females to remain in the subtidal zone while males migrate in and out of the intertidal zone (Warman *et al*., 1993; Hunter & Naylor, 1993; Reid *et al*., 1997; Styrishave *et al*., 1999). With the exception of the PL site, there is no access to an intertidal zone at the trapping sites in this study due to the presence of marina bulkheads and steep rock faces.

Audet *et al*. (2008) found that female *C. maenas* were more abundant in the springtime along the northeastern coast of Prince Edward Island, Canada. The smaller difference in proportion of females to males observed in the spring months in the present study (58.1% females to 41.9% males in the spring in contrast to an average of 74.5% females to 25.5% males in other seasons) could be due to increased foraging activity of females (Styrishave & Andersen, 2000). The fact that we captured very few gravid females is not surprising because ovigerous females tend to be inactive and burrow into soft sediment to avoid predation (Ropes, 1968; Reid *et al*., 1997; Baeta *et al*., 2006; Klassen & Locke, 2007; Audet *et al*., 2008; Fulton *et al*., 2013b). Baeta *et al*. (2006) found a higher proportion of empty stomachs in molting and ovigerous females, indicating that such females feed less. The males captured in the spring season were consistently smaller than females, a finding consistent with that of Fulton *et al*. (2013a) for crabs captured in the Great Bay and Seabrook estuaries in New Hampshire, USA. The combination of high salinity and shallow, relatively cold waters in the Salem Sound estuary likely influences the growth of the crabs overall, as both are known to play a major role in the average size increase per molt (Cadman & Weinstein, 1988). The average temperature at each site showed a positive correlation with the average seasonal CPUE suggesting that temperature has a moderate influence on the CPUE ($P < 0.01$), with large numbers of *C. maenas* captured only when the water temperature is above 5 °C.

Jensen *et al*. (2002) suggested that predatory species may limit *C. maenas* populations. In general, there are relatively few competing or predatory crustaceans present at our trapping sites, suggested by the meager by-catch of an occasional Jonah crab (*Cancer borealis* Stimpson, 1859), longwrist hermit crab (*Pagurus longicarpus* Say, 1817), Asian shore crab (*Hemigrapsus sanguineus*), spider crab *Libinia emarginata* Leach, 1815, or a juvenile American lobster (*Homarus americanus* H. Milne Edwards, 1837). CPUE was significantly higher at Hill's Yacht Yard (HYY) and Beverly Pier (BP) compared to the other three trapping sites ($p < 0.0001$), and both of these sites are characterized by very fine sediment, allowing crabs to burrow to escape predation. *Homarus americanus*, a known predator of *C. maenas* (Donahue *et al*., 2009), is more common, although not abundant, at Hawthorne Cove Marina (HCM) and PL. In addition, these two sites are somewhat shallower at low tide, making crabs more vulnerable to predation by sea gulls, whose predation of *C. maenas* (Dumas & Witman, 1993) is effective only in waters less than 1 m deep (Ellis *et al*., 2005). The substrate at Winter Island (WI) is the coarsest of any of the sites, likely due to the stronger currents in this area, and therefore not as suitable for *C. maenas* to escape predation by burrowing.

According to Jensen *et al*. (2002), physical factors such as substrate preferences could be of greater importance than interspecific competition to explain differences in habitat use. The paucity of competitive and predatory species in Salem Sound might allow *C. maenas* to occupy areas that they would not otherwise inhabit based only on physical factors such as substrate preferences. Lobsters and *Cancer borealis*, another predator of *C. maenas* (Donahue *et al*., 2009), are more common at WI than at the other sites. Competitors and predators are present and the substrate is the least suitable at WI so either or both could be responsible for the few *C. maenas* captured at that location.

Studies in Europe (e.g., Naylor, 1962; Elner, 1981; Proctor, 1997; Klassen & Locke, 2007) have reported *C. maenas* being commonly found only to depths of 5–6 m, findings that are in agreement with the present study. Novak (2004) found almost no *C. maenas* in depths greater than 7 m at his Gulf of Maine study site. Some researchers have reported that *C. maenas* can be found down to at least 10 m (Yonge, 1949; Bruce *et al.*, 1963; Green 1968; Dare & Edwards, 1981), but the number of crabs is much reduced at these greater depths (Crothers, 1968; Ingle, 1980, 1983; Clark, 1986). Our study area in Salem Sound does not exceed a depth of about 6 m so conclusions are not possible for greater depths. Only one crab was captured at a depth of 8.5 m in one of two traps that were set once in depths of 8.5 and 10.0 m at a location some distance from the study area. Average CW also showed no statistical significant difference among depths, suggesting that there are not different cohorts of crabs at different depths.

The ventral coloration of *C. maenas* captured in Salem Sound appears to be correlated with CW, with the largest crabs being red. This finding is in agreement with several studies that suggest that a decrease in molting frequency as size increases results in a longer intermolt period in red crabs *versus* green crabs, and a prolonged or terminal anecdysis in *C. maenas* accounts for the development of red coloration on the ventral surface (Carlisle, 1957; Crothers, 1967; Webster & Keller, 1986; Styrishave *et al.*, 2004; McGaw *et al.*, 1992). A higher frequency of molting results in greener crabs. Since large red males are most likely to get access to receptive females (Reid *et al.*, 1994), color variation in the *C. maenas* population, especially in the males, indicates whether the overall crab strategy emphasizes reproduction or growth (Rewitz *et al.*, 2004; Styrishave *et al.*, 2004). A strategy emphasizing growth results in green-colored crabs of both sexes due to increase in size during continuous molting, whereas a reproductive strategy invests available energy into gametogenesis and suspends ecdysis, resulting in red-colored crabs (Wolf, 1998). For any given size class, red males have larger gonads than green males so red males should be capable of fertilizing more eggs by transferring a greater amount of spermatophores to a single female or by mating with more females (Styrishave *et al.*, 2004). Larger (red) males have a competitive advantage in acquiring and mating with females over small male rivals (Van Der Meeren, 1994). The correlation between color and molting was less pronounced in our results due to the large overlap in size ranges, although crab size did increase as the coloration progressed from green to red. Slightly more red-phase crabs than green-phase crabs were larger than 60 mm CW (666 *versus* 528), whereas considerably fewer red-phase (5) than green-phase crabs (276) were smaller than 30 mm CW. Because gravid *C. maenas* limit their movements to avoid predators (Audet *et al.*, 2008), they generally do not enter traps to feed so it is not surprising that very few gravid females were captured. Of the 15 captured, 13 (86.7%) were red phase and two had a yellow ventral coloration. The size when female *C. maenas* reach maturity has been variously reported as 30 mm (Broekhuysen, 1936), 34 mm (Berrill, 1982), 30–35 mm (Styrishave *et al.*, 2004), 27–55 mm (Mohamedeen & Hartnoll, 1989), or 40–50 mm (Vinuesa, 2007). According to Berrill (1982), *C. maenas* reaches sexual maturity at smaller sizes in colder waters compared to warmer waters. He reported a maturity size of 34 mm along the Maine coast in waters somewhat colder than those along the northeastern coast of Massachusetts. One gravid female collected by us measured only 31.9 mm. If we make the reasonable assumption that crabs < 30 mm CW in Salem Sound are immature, 305 immature crabs were captured during the course of this study. The vast majority (97.7%) were green-phase crabs, whereas only 54.8% of the 7517 mature crabs (CW > 30 mm) captured were green phase. The red morphs that have been previously described from Salem Sound (Crothers, 1967; Kaiser *et al.*, 1990; McGaw *et al.*, 1992; Reid *et al.*, 1997; Abuhagr *et al.*, 2014) appear to correlate with ecdysis only after sexual maturity has been met. Sexually mature crabs follow the pattern where a longer anecdysis allows ventral coloration to transition from green to red phase (Reid *et al*, 1997). We observed that red crabs were frequently found with barnacles and slipper shells as macro-epibionts, indicative of a prolonged anecdysis, as reported by Crothers (1968). Kaiser *et al.* (1990) also reported 60% of red crabs but only 6.7% of green crabs had fouled carapaces, and 43% of red and 22% of green were infected with black necrosis. Kaiser *et al.* (1990) concluded that all red crabs are in late intermolt, whereas green crabs are in various stages of postmolt and early to mid-intermolt. Our results agree with this conclusion, but extend it to include a yellow phase (26.8% of the total crabs captured) as an intermediate life stage between the younger green phase and older red phase. Klein Breteler (1975) indicated that the interval between molts of *C. maenas* lasts longer as crabs grow older, which would allow many of the population to develop yellow coloration before they enter into a terminal anecdysis. Although red and yellow *C. maenas* share many characteristics, they perhaps should be considered as separate color phases. Of the 953 crabs with epibionts, 84.4% had some red pigmentation, being classified as either orange or red, whereas very few (6.2%) were green or yellow-green and only 9.4% were yellow, suggesting that ecdysis is most frequent in the green phase but it is more frequent in the yellow phase than in the red phase. This inference could be especially useful as a bio-indicator that could be used to predict when molting will occur in *C. maenas* in order to develop a profitable soft-shell crab market. Future studies will be needed to determine if yellow-phase *C. maenas* have distinct behavioral and physiological differences compared with green- and red-phase crabs, as seen between the green and red phases (e.g., Ameyaw-Akumfi & Naylor, 1987; Reid & Aldrich, 1989; McGaw & Naylor, 1992c; Reid *et al.*, 1997; Rewitz *et al.*, 2004).

In a study that examined how color plays a role in behavior and molting, Fulton *et al.* (2013b) found that females were the reddest in the summer (72.3%), and the greenest in the fall (65.0%), and males had the reddest colors in spring and fall. Similar results were seen in the present study, where red-phase females were most common in the spring and green phase in the fall whereas males were reddest in the spring and fall and greenest in the summer. Both sexes appear to be devoting resources to reproduction in the spring, with ecdysis being suspended, whereas molting and growth predominates in males during the summer and in females during the fall months.

The largest numbers of *C. maenas* were captured at sites with very fine sand (0.0625–0.125 mm), perhaps because this sediment size is most conducive to their burrowing behavior (Ropes, 1968). Pebble-type sediment (4–64 mm) could favor crabs with a darker, redder color, as indicated by the higher CI value (mean 6.5 mm) in the crabs captured in that habitat, whereas medium-size sand (0.25–0.50 mm) and coarse to very coarse sand (0.50–2 mm) are both bottom types where green-phase crabs were more common. Stevens *et al.* (2014) noted that brightness, saturation, and even habitat are excellent predictors of life stage in *C. maenas* and juvenile crabs are capable of changing luminance to be more cryptic in their environment. Pebble sediment certainly provides a variable environment, suggesting that crabs seek out sediment that is cryptic for protection. Comparatively few *C. maenas* were captured at WI, where *C. borealis* and *H. americanus*, known predators of *C. maenas* (Elner, 1981), were most common as by-catch.

Although the large "Blanchard" trap captured the most crabs of the traps evaluated, there are other considerations when choosing a trap. The "Blanchard," "slanted-sides," and "Terminator" traps all would be good to use in a commercial venture, especially in waters with strong currents, if the collecting boat and transport vehicle is of sufficient size. The "trapezoidal" trap has a low profile and moderate weight, is reasonably easy to transport, catches a large number of crabs, and is recommended for commercial trapping or large-scale efforts to reduce the *C. maenas* population in a particular area. The "Ketcham" trap is small enough to be easily transported and hauled, but it does not have the capacity of the previous traps, so is recommended in areas where crab density is low. The eel and minnow traps are designed to catch fish, and therefore are not recommended to capture *C. maenas*.

Carcinus maenas is known to be nonselective in its diet when food is sparse, with recorded prey items varying from plant and algal material to bivalves and barnacles (Ropes, 1968; Cohen *et al*., 1995; Jensen *et al*., 2002). The bait used must be effective, readily available, and inexpensive for commercial trapping. Bivalves make up the majority of the natural diet, but the use of shellfish as bait is not practical. Of the various fish baits evaluated, the highest number of *C. maenas* was captured with herring, an oily fish that presumably could attract crabs from some distance. Metabolites exuding from prey are detected by the antennae and crabs follow the edge of an odor plume (Zimmer-Faust *et al*., 1995) until visual and tactile detection (Hughes & Seed, 1995). Although herring is identified as the best bait based on this study, other types of bait could be used. Herring may not always be available and it must be purchased from a bait store so any commercial venture must show sufficient return to offset this initial expense. Therefore, it might be more practical and economical for crabbers to use whatever fish carcasses are readily available from fish markets at minimal or no cost.

An increase in the population of *C. maenas* along the New England and Canadian Atlantic coastlines is of considerable concern to the lucrative soft-shell clam *Mya arenaria* industry, and therefore, methods to reduce the crab population are of great interest. Trapping is the only feasible way to catch *C. maenas* in most cases and has proven to be moderately successful at reducing the population in some locations, for example Kejimkujik National Park Seaside in Nova Scotia, Canada (McCarthy, 2013). Trapping just to remove crabs must be subsidized by governmental or other funding to make it economically worthwhile for crab fishers. A commercial industry based on *C. maenas* would be more effective at controlling the population because it would be profitable to catch crabs. Some crabs are trapped for use as fish or conch bait but this represents a small fraction of the population. It is possible to utilize crab-shell chitin for fertilizer, as well in the production of self-healing car paints (Ghosh & Urban, 2009) and inexpensive anti-viral drugs (Steiger *et al*., 2011). Despite *C. maenas* long being considered to be of little value as a food item (Broekhuysen, 1936), the possibility of using this species for food has recently gained interest. The information presented here concerning seasonal CPUE, size, coloration as it pertains to molting, and merits of traps and baits should be useful for establishing a financially viable commercial use of *C. maenas* as a source of bait and food for human consumption.

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