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A comparison of the distribution and abundance of European green crabs and American lobsters in the Great Bay Estuary, New Hampshire, USA

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**Highlights**

• Distribution and abundance of invasive green crabs to determine impact on lobster populations.

• Green crabs were found in warm, low salinity regions while lobsters were in colder, more saline areas.

• In lab trials, lobsters were more aggressive than green crabs, except adult green crabs paired with small lobsters.

• Data suggest that green crabs could have a moderate impact on lobster populations in estuaries.


## ABSTRACT

Green crabs (*Carcinus maenas)* are an invasive species documented as having negative impacts on the biota of marine and estuarine communities. However, their impact on the American lobster (*Homarus americanus*) is not well understood. During a two-year trap study (2013 - 2014) in The Great Bay Estuary, NH, we captured 1,229 green crabs and 144 lobsters in 248 individual trap hauls (average catch per unit effort = 10.98 ± 1.51 for green crabs and 0.49 ± 0.08 for lobsters), or ~ 8.5 times more green crabs than lobsters. In general, green crabs were more abundant in areas furthest from the coast, which also tended to be warmer, while lobsters were more abundant in areas closer to the coast. Nevertheless, there was still considerable overlap between the two species. We evaluated the competitive interactions between green crabs and lobsters in the laboratory using a behavioral assay and found that in 31% of the trials, large lobsters (> 80 mm in carapace length) killed (and consumed) green crabs of varying sizes that failed to escape or move to safe areas of the enclosure. These results suggest that adult lobsters are not likely vulnerable to green crabs. While there may be reasons why lobsters did not select specific sizes of green crabs to prey on, some crabs may have an impact on juvenile lobsters. These data provide some insight into the distribution and abundance of green crabs and their

impact on the lobster population in a large New England estuary that supports a commercial lobster fishery.

## 1. Introduction

Species range expansions and contractions are in constant flux and are under the influence of both biological and physical factors (Brown et al., 1996). The ability to provide better spatial resolution to distribution patterns of native and non-indigenous (i.e. exotic, invasive) species can provide insight into the relative contributions of ecological and physical factors in shaping these patterns (Ruiz et al., 1997; 1999). Historically, biological responses to non-indigenous species were due to natural processes and often occurred over long (geological) time scales (reviewed in Lonhart, 2009). However, anthropogenic- and climate-mediated processes have played increasingly disproportionate roles in driving shifts in the distribution of invasive species (Ruiz et al., 1997; Cohen and Carlton, 1998; Kennish, 2002).

Traditionally, marine invasions have concentrated on estuarine habitats (see Ruiz et al., 2000, Preisler et al., 2009 for review). Estuarine systems are especially vulnerable to high rates of invasions for three primary reasons: (1) they are often sites of intensive human activity (e.g. shipping, aquaculture, pollution, diking) to which natives are not well-adapted (Cohen and Carlton, 1998; Kennish, 2002); (2) low species richness in estuaries usually translates into high invasion rates due to weak competitive interactions with native species (Wolff, 1999) and; (3) the hydrodynamics of many estuaries (e.g. semi-enclosed circulation) facilitates the retention of many meroplanktonic larvae, both native and invasive (i.e. founder populations, Wasson et al., 2005; Roman, 2006).

Invasions by brachyuran crabs have negatively influenced marine and estuarine communities world-wide and pose legitimate economic and ecological threats (Carlton and Geller, 1993). One such example is the predatory invasive portunid green crab (*Carcinus maenas*), which has established breeding populations outside its native European range and has since become a common (naturalized) species in New England and the Canadian Maritimes (reviewed in Edgell and Hollander, 2011). Green crabs alter architecturally-complex estuarine habitats (e.g. eelgrass, *Zostera marina*) through bioturbation (Garbary et al., 2014) and have a negative impact on both mussel (*Mytilus edulis*) and oyster (*Crassostrea virginica*) beds (DeGraf and Tyrell, 2004; Miron et al., 2005).

As predators, green crabs are formidable consumers of a wide variety of benthic marine macrofauna (Mascaró and Seed, 2001) and, in New England waters, have been implicated in declines of soft-shelled clam (*Mya arenaria*) populations (e.g. Bryan et al., 2015). *C. maenas* has also been known to prey upon juvenile fishes (e.g. winter flounder, *Pseudopleuronectes americanus*; Fairchild et al., 2008) and compete with American lobsters (*Homarus americanus*) for space (Rossong et al., 2006; Williams et al., 2006; Haarr and Rochette, 2012). More recently, it was shown that green crabs have the ability to curtail the overall foraging activity and shelter use of small (< 35 mm carapace length) juvenile lobsters (Rossong et al., 2011), and prey upon newly settled lobsters (Sigurdsson and Rochette, 2013). Although they are euryhaline organisms and are most commonly distributed throughout coastal and offshore waters (Lawton and Lavalli, 1995), American lobsters are also known to reside in estuarine habitats from Canada to New England. The Great Bay Estuary (herein, GBE) in New Hampshire is home to a year-round lobster population which is a target commercial fishery in the bay (NHFG, 2008; Morrissey, 2016).

The GBE is facing environmental threats (e.g. pollution, coastal development, invasive species, climate change) similar to many other estuarine systems (Kennish, 2002; Oviatt, 2004; PREP, 2014). In recent years, GBE has undergone dramatic ecological changes due, in part, to a cascade of factors that include increases in water temperatures, nitrogen loading, and the degradation of important habitats such as oyster reefs and eelgrass beds (PREP, 2014). It is thought that estuaries may provide resident lobsters with benefits that include accelerated growth and molting cycles (due to warmer temperatures), protection from predation, and reproduction and nursery habitats (Munro and Therriault, 1983; Becker, 1994; Moriysu et al., 2000, Short et al., 2001, Morrissey, 2016). Both lab and field studies indicate that lobsters can detect small changes in both temperature and salinity and these may guide their seasonal movements in GBE (Jury et al., 1994a; Crossin et al., 1998; Watson et al., 1999; Jury and Watson, 2000). Recent studies further suggest that, because of its highly recessed basin system and hydrodynamic profile, GBE may serve as a sink for postlarval settlement and as a nursery ground for small, juvenile lobsters (Goldstein, 2012; Morrissey, 2016).

Green crabs have firmly established themselves in GBE and other New England estuarine systems for decades (Hayden and Conkling, 2014). Interestingly, the only systematic survey of green crabs in GBE was completed by Fulton et al. (2013) in 2009-2010. During this one-year study, ~ 0.09 metric tons of green crabs were captured, yielding higher capture rates in the spring and fall and concentrated in the middle section of GBE (i.e. Little Bay). This survey concluded that these spatial and temporal differences in catch were likely due to fluctuations in temperature and salinity (Fulton et al., 2013). While this study provided notable information about the green crab population in GBE, it was not designed to compare the distribution of green crabs with lobsters (only 29 lobsters were collected in total).

Given the importance of the lobster fishery in GBE, along with the continued trend in climate-mediated changes to estuarine communities, a more thorough understanding of this crab-lobster relationship is warranted. Thus, in this study we (1) determined the distribution and size structure of lobsters and green crabs in GBE and; (2) began to examine the behavioral interactions of these two species when placed together in the laboratory.

## 2. Materials and methods

### *2.1. Study Site*

The Great Bay Estuary (GBE) is a large, tidally mixed basin that is comprised of ~ 23 $km^2$ of surface water and over 160 km of coastline. Great Bay is 15-25 km from the coast and is coupled to the ocean through Little Bay and the Piscataqua River in New Hampshire and Maine (Jackson, 1922; Short, 1992; Fig. 1). Both Great Bay (GB) and Little Bay (LB) possess habitats that are generally characterized by eelgrass beds, extensive mud flats, and oyster reefs (Grizzle et al., 2008) with freshwater input from seven rivers that intermingle with tidal waters, influencing salinity levels, especially after severe episodic events. Both temperature (-1 to > 20 °C,) and salinity (0 - 35 psu) may drastically fluctuate at varying spatio-temporal scales (Jury and Watson, 1994b). These fluctuations, in turn, set up a dynamic gradient in environmental conditions with which to compare the distribution and abundance of green crabs and lobsters. Our field survey locations (Fig. 1) were selected based on empirical data from past studies (see Jury and Watson, 2013), so as to evaluate the distribution of these two species in a zone of overlapping distribution.

### *2.2. Field surveys*

A trap study was conducted during June-August of 2013 and 2014 (three months in total over each of two seasons) throughout selected sites in Great Bay and Little Bay. Trap trawls (i.e. trap transects) were fished at four fixed sites along a spatial gradient (coastal to estuarine in GBE; Fig. 1). Trawls comprised two trap types: 1) standard ventless lobster traps (see Clark et al., 2015 for design details) and; 2) juvenile collectors, which were made from ventless traps that were modified with a 47 cm square tunnel entrance device (Protoco Enterprises, Inc., North Plains, OR) used to select for small crabs and lobsters.

All trap trawls (four sets in total) were fished along similar depth contours (range = 5-8 m) and were pulled every 2-5 days (i.e. soak time) for each of two years (2013-2014) from June through August. It is important to note that there is evidence to suggest that soak time does, in fact, influence both lobster and crab catch (see Richards et al. 1983; Miller et al. 1995). In a preliminary study, we did not find any apparent difference in lobster catch ($W = 7.42$, $P = 0.283$) or carapace length (ANOVA, $P = 0.58$) over the range of soak times (2-5 days) that we chose using the same suite of trap designs. However, there were differences in crab catch ($W = 21.32$, $P = 0.002$) and carapace width over this same time frame ($P = 0.003$), which likely results from both a greater number of crabs and larger crabs captured in 2013. All traps were fished in the same locations and baited with equal amounts of herring (*Clupea harengus*). Temperature data loggers (HOBO model UA-002-64, Onset Computer, Bourne, MA) were affixed to each trawl to record water temperature at 30-minute intervals.

Lobster and green crab catch were enumerated and the sex of each individual was determined for each trap haul. The carapace length (lobster) and carapace width (crab) for a randomized subsample ($n = 10$/trap/trial) of each species were measured to the nearest mm using calipers. Carapace length (CL) or width (CW) data were used to predict weights based on a regression analysis (see section 2.3), and the relative abundance was calculated using catch-per-unit-effort (CPUE, the number of animals / trap haul). Because our data violated the assumptions of normality and heterogeneity of variance we compared the differences in crab-lobster abundance by each year at the different sites using a non-parametric Wilcoxon signed-rank test (*W*, Zar, 1999). All statistical tests were carried out using the statistical software package JMP v.11.21.1 (SAS Institute, Cary, BC).

### *2.3. Weight-length (W-L) relationships*

For a subsample of both lobsters (10 males and 13 females, $n_{total}$ = 23) and crabs (61 females and 9 males, $n_{total}$ = 70), we recorded individual weights using an analytical balance (Ohaus Scout SPX622, Ohaus Corp., Parsippany, NJ) along with CL and CW. Only crabs and lobsters with a full complement of claws and legs were used. Regressions of weight vs. length were modeled using JMP, and data were fit using the methods outlined in Krouse (1973). An analysis of covariance (ANCOVA, factor 1 = sex; factor 2 = length, dependent variable = weight) was selected to examine the effect of sex on the W-L. relationship. These regressions were then used to calculate estimated weights of lobster and green crabs captured during 2013 and 2014 and the overlap and size were compared between the two species. The calculated regression equations were as follows:

(a) Female green crabs: $Log\ 10\ W = -3.2687 + 2.7908\ Log10L, (R^2 = 0.934)$
(b) Male green crabs: $Log\ 10\ W = -3.4578 + 2.9184\ Log10L, (R^2 = 0.933)$
(c) Lobsters: $Log\ 10\ W = -2.7894 + 2.8319\ Log10L, (R^2 = 0.987)$

*2.4. Behavioral assays*

To gain a better understanding of the potential interactions between green crabs and lobsters, a series of paired predator/prey trials were conducted at the UNH Jackson Estuarine Laboratory located on GBE (Durham, NH) from June through August, 2014. We paired individual crabs and lobsters in a size-assorted matrix ($n$ = 36 paired predation trials; Table 1) based on the range of sizes that we caught throughout our trap surveys (section 2.2). For each trial, a single large individual was paired with a smaller individual of the other species. Because we were purposely testing forced exchanges in our trials, neither food nor shelter was provided for the duration of any given trial (48 hrs. in total). Each lobster-crab pair was placed inside a 91 cm diameter ring that was submerged inside a larger 1.8 m diameter round fiberglass tank that was connected to an ambient flow of seawater from GBE. The periphery of the tank was shrouded in black plastic to allow a controlled (12:12, light:dark) cycle. Red light was used at night to allow the camera system to capture time-lapse video. All trials were recorded using a self-contained digital time-lapse camera (Brinno TLC200 HD video camera, Taipei City, Taiwan) that was set to a capture one frame every two seconds. All video data were downloaded at regular intervals from a SD card and transferred onto a laptop computer. Video footage was later analyzed using the playback software QuickTime 7 (Apple Inc., Cupertino, CA). Each video was examined to confirm if either the crab or the lobster escaped from their enclosure. Video data were compared as the percentage of trials where lobsters were killed, escaped or were alive using a goodness-of-fit test ($G$-test), and mean size of crabs in each group was compared using a series of t-tests.

**3. Results**

*3.1. Catch and size data*

Trap trawls were hauled a total of 17 times in 2013 and 14 times in 2014 ($n_{total}$ = 31 hauls, and 248 traps examined). During 2013, 59 lobsters were captured, as well as 451 male green crabs and 365 female green crabs. In 2014, 85 lobsters, 162 male green crabs and 251 female green crabs, were caught. Overall, for the two years combined, we trapped ~ 8.5 times more green crabs than lobsters. The average weight of lobsters caught in 2013 was 314.3 ± 18.3 g and in 2014 it was 289.8 ± 16.1 g, and these were not different from year-to-year (t-test, $P$ = 0.316, Table 2).

The average size of male green crabs captured in 2013 was 82.0 ± 1.3 g and in 2014 it was 74.4 ± 2.0 g, and these sizes were different between years (t-test, $P$ = 0.0004). The female green crabs captured in 2013 were significantly smaller in 2013 vs 2014 (50.1 ± 1.0 g and 54.4 ± 0.9 g, respectively; t-test, $P$ = 0.002, Fig. 2).

*3.2. Weight-Length (W-L) relationship*

The relationship between size and weight was more pronounced in lobsters than green crabs, but that is likely due to the larger range of lobster sizes examined. There was an effect of sex in green crabs, and data were not combined (Sex*CW, $P$ = 0.0002); however, there was no effect of sex on size for lobster (Sex*CL, $P$ = 0.12) and therefore lobster data were pooled (Fig. 3). The significant difference in sex as a variable for green crabs may be a result of a small sample size of male crabs; generally, the weight-length relationships were similar. The calculated weight-length relationship for lobster was similar to that created by Krouse (1973), to obtain an estimated relationship of: log $W = -2.9052 + 2.9013 \, Log \, L$ (also see methods section 2.3).

*3.3. Catch-per-unit-effort (CPUE)s*

Catch (CPUE) between the two years was different for lobster and significantly more lobsters were captured during the 2014 trap study ($W = 5.16$, $P = 0.0231$). Significantly more green crabs were captured during 2013 study as compared to 2014 ($W = 17.564$, $P = < 0.0001$). Catch data for both species were analyzed separately, and comparisons were only made within years (Fig. 4, Table 3). During both years of the trap study, more lobsters were captured in Little Bay than Great Bay ($W = 56.36$, $P = <0.0001$). Green crabs were generally captured in higher numbers in Great Bay; however, there were a few days of very high catch of crabs in Little Bay sites during 2013. As a result, there were significantly more crabs captured in Little Bay in 2013 than in Little Bay during the 2014 trap study ($W = 20.89$, $P = < 0.0001$). Green crab abundance was similar in Little Bay and Great Bay during the 2013 trap study ($W = 0.002$, $P = 0.966$). During the 2014 trap study, significantly more green crabs were captured in Great Bay than in Little Bay ($W = 33.73$, $P = < 0.0001$).

*3.4. Behavioral data*

In 31% of the trials (11/36) green crabs were consumed by lobsters. There was no difference in the average size of green crabs that were killed and eaten (60.3 ± 7.4 g) in comparison to those that survived (*n* = 34, 53.2 ± 7.62, *G*-test , *P* = 0.51). Lobsters that ate green crabs tended to be slightly larger (471.8 ± 49.1 g) than those that did not eat green crabs (347.7 ± 34.8 g); however, there were no significant differences in size (*n* = 34, t-test, *P* = 0.053). Two trials were conducted with juvenile lobsters (< 16 mm CL, < 4.2 g) and large green crabs (< 75 mm CW, > 103 g) to determine if larger green crabs were able to consume smaller lobsters. In one of these trials, the green crab ate the lobster, and in the other, the lobster was able to escape from the enclosure. In the remaining trials, green crabs managed to escape from the enclosure 44% of time (16/36), and were alive inside the enclosure with the lobster at the end of the 48-hour period 19% (7/36). Crabs that survived were often found avoiding the lobster by clinging to the enclosure above the water level (video observations).

*3.5. Temperature data*

We compared temperature data from June-August in 2013 and 2014 and found that there was a significant difference in the mean temperature between both years at all four study sites (unpaired t- test, *P* = <0.0001). Therefore, the data were not pooled, and temperature data were analyzed separately by year. Despite differences in overall temperature between years, the trends were similar. Water temperatures in Great Bay (Adams Point and Nannie Island, Fig. 1) were warmer than in Little Bay by ~ 2$^{o}$C (Fig 5). In 2013, water temperatures were progressively cooler towards the coast ranging from 21.15 ± 0.21$^{o}$C up-estuary to 18.80 ± 0.19$^{o}$C down-estuary. In 2014, the water temperatures in Great Bay were very similar to our 2013 values, (21.4 ± 0.13 and 21.6 ± 0.10 $^{o}$C, Tukey's HSD test *P* = 0.894 ) and were significantly warmer (one-way ANOVA, *P* = <0.0001) than in Little Bay (19.35 ± 0.18$^{o}$C vs 18.84 ± 0.17$^{o}$C, Tukey's HSD test $P$ = 0.074). However, there was not a strong relationship between water temperatures and green crab catch in 2013 ($R^2$ = 0.024) or with lobster catch ($R^2$ = 0.069).

## 4. Discussion

The American lobster is a prominent marine crustacean in GBE, unlike in many other estuaries (Jury and Watson, 2013). However, the interactions of lobsters along with a growing population of green crabs, remains largely unstudied. The goal of this study was to begin to quantify and describe overlapping patterns of lobster and green crab distribution in GBE and to understand why distributional differences might occur.

### *4.1. Lobster-crab behavioral assays*

Our behavioral assays clearly demonstrated that larger lobsters dominate smaller green crabs and either cause them to flee, or they capture and consume them. It is important to note that, because we collected animals for these trials from the lobster trap survey, we were unable to fully represent the entire spectrum of sizes for both species in our paired trials. In particular, our trials did not include small juvenile green crabs, as they were able to pass through the mesh of the trap. It is likely that these smaller green crabs would be even more susceptible to lobster predation. Likewise, we were unable to capture enough small lobsters to pair with larger green crabs, but the data we did collect suggests that adult green crabs could have an impact on newly settled and juvenile lobsters in GBE. This conclusion is more consistent with studies by Rossong et al. (2006) and Sigurdsson and Rochette (2013), which also documented large green crabs preying on juvenile and newly settled lobsters. Conducting more of these studies would allow us to understand if this case was an anomaly or if large green crabs consume juvenile lobsters more frequently.

While we purposefully conducted our study to force interactions demonstrating that predation is possible between these two species, further research dealing with the connections of these species in a more natural setting (i.e. mesocosm) would be very useful. Williams et al. (2006) found that when green crabs and lobsters were simultaneously released into a tank with one food item, green crabs were better at reaching the food first and defending it from lobsters. However, when lobsters were released first, they were able to reach the food first and defend it from crabs. The interface between green crabs and lobsters can elicit further complex exchanges that are collectively referred to as intraguild predation (IGP) or a special case of both competition and predation, distinguished by 'the immediate energetic gains for one participant (the predator)' (reviewed in Polis et al. 1989). As such, IGP may influence a variety of life-history traits (e.g., brood size, growth) that, in turn, may significantly impact the distribution, abundance, and even evolution of many species. Empirical evidence for both individual- and population-level implications of IGP are seen in invertebrates, birds, and mammals (Polis et al. 1989) and may be a possible mechanism for green crab-lobster interactions. The timing of the animals' release would have to be taken into consideration in future trials, and would help show which interspecific exchanges (i.e. predation or competition) occur more frequently between the two species in our study area. This work may also shed light on why lobsters consumed green crabs and if there is a targeted or preferred size range. Furthermore, if competition drives community parameters (e.g. Molis and daGama, 2009), size may not play a role in the depletion of resources affecting these species.

*4.2. Differences in lobster-crab distributions in GBE*

One of the most interesting results of our study was the much greater abundance of green crabs in the upper reaches of the GBE compared with lobsters (Fig. 4). This green crab distribution pattern was in general agreement with the data reported by Fulton et al. (2013). It should be noted however, that the former study used a different type of trap fished for a shorter soak time (~ 24 hrs.).

The ongoing invasive success of *Carcinus maenas* is due, in large part, to its ability to tolerate a wide range of environmental conditions. In fact, green crabs are one of the most euryhaline brachyuran crabs and have been shown in laboratory studies to tolerate salinities as low as 8 psu (Henry et al., 1999). Surveys of green crabs in some U.K. estuaries reported that these animals were most commonly found in the largest numbers within the median of a large salinity gradient (e.g. Mathieson and Berry 1997). This tolerance to low salinities may explain, in part, why the largest numbers of green crabs obtained in our study were caught in Great Bay, which tends to have a lower salinity than locations closer to the coast. Two other studies (Howell et al., 1999; Goldstein, 2012) found that significantly more lobsters were captured further down-estuary in the Piscataqua River (see Fig. 1), which was also the case in Narragansett Bay, Rhode Island (Wahle, 1993). The likely mechanism underlying the salinity tolerance of green crabs is due to phenotypic plasticity whereby *C. maenas* can alter its physiology, behavior, and morphology to better match changing environmental conditions (Henry et al., 1999). Invasive species, like green crabs, may benefit from phenotypic plasticity if it allows them to thrive in a wider range of environmental conditions than they could when having non-plastic traits specialized for conditions unique to their native range (Braendle and Flatt, 2006). By contrast, limited osmoregulators, like lobsters, are more physiologically-challenged by changes in salinity and tend to avoid areas with lower salinities. For example, adult lobsters vacate their shelters at salinities < 12 psu and prefer higher salinities (> 25 psu) to lower ones (Jury et al., 1994a). This is likely due to the increased metabolic demands of osmoregulating (Jury et al., 1994b).

Another major environmental factor that might be responsible for influencing the distribution of lobsters and green crabs in GBE is water temperature. It is well known that lobsters can sense small changes in temperature (Jury and Watson, 2000) and show thermal preferences (15.9 °C), avoiding water that is either too cold or too warm (< 5 °C and > 18 °C; Crossin et al., 1998). Much less is known about the thermal preferences of green crabs, although it is thought that this species has a comparatively wider thermal tolerance (0-30 °C; Cohen and Carlton, 1998; Kelley, 2014). Therefore, while lobsters tend to avoid warm water, because temperatures in excess of ~ 20.5 °C lead to significant thermal and metabolic stress (Dove et al., 2005), green crabs might actually favor warmer water, which may promote increased growth and maturation. Therefore, our working hypothesis is that green crabs in GBE select locations that reflect temperature and salinity ranges where competition with other crustacean species is lower and that this tendency may separate these species enough to minimize interspecific interactions during parts of the year (summer), but maybe not others (winter).

Water temperatures in GBE are warming at unprecedented rates (Trowbridge, 2006; Dijkstra et al., 2011; PREP, 2014) and this has enabled a significant number of green crabs and some blue crabs (e.g. *Callinectes sapidus,* Johnson, 2015) to expand their ranges to colonize waters that were once too cool to sustain them. Determining the distribution of invasive crab species in GBE, and their ability to prey upon economically important species (e.g. oysters and lobsters), is critical for predicting their ecosystem impact including competition for resources (e.g. shelter, food). Data from the Fulton et al. (2013) study found that green crabs in GBE were significantly larger (carapace size, weight) than those in another regional estuary (Hampton-Seabrook Estuary, NH). The higher temperatures in GBE may result in larger crab size due to faster growth rates, and in warming climate scenarios, individual crabs may attain even greater sizes, thus negatively impacting lobster populations (Fulton et al. 2013). Only through ongoing monitoring efforts and the continued collection of 'baseline' data will we fully understand the dynamics that drive these processes.

Although the bathymetry and general habitat features of GBE have been mapped (CCOM-JHC 2010), other more localized efforts suggest that habitat composition is markedly different between up- and down-estuary areas (NHFG, 1998; Becker, 1994; Grizzle et al., 2008; Goldstein, 2012). These studies also demonstrated that small lobsters have an affinity for complex habitats. Becker (1994) found that > 50 % of all lobsters collected in dive surveys were between 40 – 60 mm CL, suggesting that juvenile lobsters may reside in specific regions of preferred habitat in GBE. Identifying which locations in GBE that provide specific habitats conducive for lobster settlement and juvenile residence are important correlates to understanding further interactions with green crabs. It remains to be seen if habitat preference or predator-prey interaction (i.e. intraguild predation) is the driving force behind the distribution of green crabs and lobsters in GBE. Juvenile lobsters in the upper reaches of the estuary may be subject to predation by larger green crabs and conversely, small crabs down-estuary face predation by adult lobsters. Determining these relationships will help the continued sustainability of the lobster fishery in Great Bay Estuary.

## 5. Conclusions

Like many other estuaries in New England, the Great Bay Estuary in New Hampshire is now home to a large population of green crabs. The overall goal of this study was to determine how green crabs might interact with, and impact, resident lobsters. First, we found that green crabs are most abundant in the lower salinity, warmer water in areas further up into the estuary, while lobsters were found in the greatest numbers in areas closer to the coast. This distributional pattern is likely to limit the extent to which green crabs and lobsters directly interact with each other, or compete for resources. Based on our behavioral assays, when lobsters encounter green crabs, lobsters are likely to be the dominant species. However, in areas where they do overlap, green crabs tended to be larger (by weight) than the lobsters, so they could have an impact on the lobster fishery in the estuary. We believe the findings from this study are important in future studies between these species under a changing climate scenario and for assessing the potential impact of green crabs on the lobster fishery.

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## 7. References

Braendle, C., Flatt, T. 2006. A role for genetic accommodation in evolution? BioEssays 28, 868-873.

Becker, C.J. 1994. The influence of prey availability and habitat structure on the distribution of lobsters (*Homarus americanus*) in the Great Bay Estuary. M.Sc. thesis, Department of Zoology, University of New Hampshire, Durham, N.H.

Brown, J.H., Stevens, G.C., Kaufman, D.M. 1996. The geographic range: Size, shape, boundaries and internal structure. Ann. Rev. Ecol. Sys. 27, 597-623.

Bryan, E., Tan, P., Beal, B.F. 2015. Interactions between the invasive European green crab, *Carcinus maenas* (L.), and juveniles of the soft-shell clam, *Mya arenaria* L., in eastern Maine, USA. J. Exp. Mar. Biol. Ecol. 462, 62-73.

Carlton, J.T., Geller, J.B. 1993. Ecological roulette: The global transport and invasion of nonindigenous marine organisms. Science 261, 78-82.

Center for Coastal and Ocean Mapping (CCOM)-Joint Hydrographic Center. 2010. University of New Hampshire, Durham, NH: Project website. http://ccom.unh.edu/index.php?page=home.php&p=42&page=great_bay.php.

Clark, A.S., Jury, S.H., Goldstein, J.S., Langley, T.G., Watson, W.H. III. 2015. A comparison of American lobster size structure and abundance using standard and ventless traps. Fish. Res. 167, 243-251.

Cohen, A.N., Carlton, J.T. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279, 555-558.

Crossin, G., Al-Ayoub, S.A., Jury, S.H., Howell, W.H., Watson, W.H. 1998. Behavioral thermoregulation in the American lobster (*Homarus americanus*). J. Exp. Biol. 201, 365-374.

DeGraaf, J.D., Tyrell, M.C. 2004. Comparison of the feeding rates of two introduced crab species, *Carcinus maenas* and *Hemigraspus sanguineus*, on the blue mussel, *Mytilus edulis*. Northeast. Nat. 11, 163-166.

Dijkstra, J.A., Westerman, E.L., Harris, L.G. 2011. The effects of climate change on species composition, succession and phenology: A case study. Glob. Change Biol. 17, 2360-2369.

Dove, A.D.M., Allam, B., Powers, J.J., Sokolowski, M.S. 2005. A prolonged thermal stress experiment on the American lobster, *Homarus americanus*. J. Shell. Res. 24, 761-765.

Edgell, T.C., Hollander, J. 2011. The evolutionary ecology of European green crab, *Carcinus maenus*, in North America. in: Galil, B.S., Clark, P.F., Carlton, J.T. (Eds.), In the Wrong Place - Alien Marine Crustaceans: Distribution, Biology and Impacts, Invading Nature. Springer Series in Invasion Ecology 6, New York, pp. 642-659.

Fairchild, E.A., Rennels, N., Howell, W.H. 2008. Predators are attracted to acclimation cages used for winter flounder stock enhancement. Rev. Fish. Sci. 16, 262-268.

Fulton, B.A., Fairchild, E.A., Warner, R. 2013. The green crab *Carcinus maenas* in two New Hampshire estuaries. Part 1: Spatial and temporal distribution, sex ratio, average size, and mass. J. Crust. Biol. 33, 25-35.

Garbary, D.J., Miller, A.G., Williams, J, Seymour, N.R. 2014. Drastic decline of an extensive eelgrass bed in Nova Scotia due to the activity of the invasive green crab (*Carcinus maenas*). Mar. Biol. 161, 3-15.

Goldstein, J.S. 2012. The impact of seasonal movements by ovigerous American lobsters (*Homarus americanus*) on egg development and larval release. Ph.D. dissertation, University of New Hampshire, Durham, NH. 332 p.

Grizzle, R.E., Brodeur, M.A., Abeels, H.A., Greene, J.K. 2008. Bottom habitat mapping using towed underwater videography: subtidal oyster reefs as an example application. J. Coast. Res. 24, 103-109.

Haarr, M.L., Rochette, R. 2012. The effect of geographic origin on interactions between adult invasive green crabs *Carcinus maenas* and juvenile American lobsters *Homarus americanus* in Atlantic Canada. J. Exp. Mar. Biol. Ecol. 422-423, 88-100.

Hayden, A., Conkling, P. 2014. What is changing in the Gulf of Maine? National Fisherman. June 2014, 7-8.

Henry, R.P., Garrelts, E.E., McCarty, M.M., Towle, D.W. 1999. Salinity adaptations in the euryhaline green crab, *Carcinus maenas*. Bulletin – Mount Desert Island Biological Laboratory, 38, 55.

Howell, W.H., Watson, W.H. III, Jury, S.H. 1999. Skewed sex ratio in an estuarine lobster (*Homarus americanus*) population. J. Shell. Res. 18, 193-201.

Jackson, C.F. 1922. Ecological features of Great Bay, New Hampshire and a preliminary checklist of its fish. Ecology, 3, 48-54.

Johnson, D.S. 2015. The savory swimmer swims north: A Northern range extension of the blue crab *Callinectes sapidus*? J. Crust. Biol. 35, 105-110.

Jury, S., M.T. Kinnison, W.H. Howell, and W.H. Watson III. 1994a. Metabolic responses of lobsters exposed to reduced salinity. J. Exp. Mar. Biol. Ecol. 176, 167-185.

Jury, S.H., Kinnison, M.T., Howell, W.H., Watson, W.H. 1994b. The behavior of lobsters in response to reduced salinity. J. Exp. Mar. Biol. Ecol. 180, 23-37.

Jury, S.H., Watson, W.H. III. 2000. Thermosensitivity of the American lobster, *Homarus americanus*. Biol. Bull. 199, 257-264.

Jury, S.H., Watson, W.H. III. 2013. Seasonal and sexual differences in the thermal preferences and movements of American lobsters. Can. J. Fish. Aquat. Sci. 70, 1650-1657.

Kelley, A.L. 2014. The role thermal physiology plays in species invasion. Conserv. Physiol. 2, doi:10.1093/conphys/cou045.

Kennish, M.J. 2002. Environmental threats and environmental future of estuaries. Environ. Conserv. 29, 78-107.

Krouse, J.S. 1973. Maturity, sex ratio, and size composition of the natural population of American lobster *Homarus americanus*, along the Maine coast. Fish. Bull. 71, 165-173.

Lawton, P., Lavalli, K.L. 1995. Postlarval, juvenile, adolescent, and adult ecology. In: Biology of the lobster *Homarus americanus* Factor, J.R. (Ed.), Academic Press, San Diego, pp. 47-81.

Lonhart, S.I. 2009. Natural and Climate Change Mediated Invasions. in: Rilov, G, Crooks, J.A. (Eds.), Biological Invasions in Marine Ecosystems. 57 Ecological Studies 204, Springer-Verlag, Berlin, pp. 57-69.

Mathieson, S., Berry, A. 1997. Spatial, temporal and tidal variation in crab populations in the Forth Estuary, Scotland. J. Mar. Biol. Assoc. U.K. 77, 167-183.

Miller, R.J., Addison, J.T. 1995. Trapping interactions of crabs and American lobster in laboratory tanks. Can. J. Fish. Aquat. Sci. 52, 315-324.

Miron, G., Audet, D., Landry, T., Asu, M.M. 2005. Predation potential of the invasive green crab (*Carcinus maenas*) and other common predators on commercial bivalve species found on Prince Edward Island. J. Shell. Res. 24, 579-586.

Mascaró, M., Seed, R. 2001. Foraging behavior of juvenile *Carcinus maenas* (L.) and *Cancer pagurus* L. Mar. Biol. 139, 1135-1145.

Molis, M., daGama, A.P. 2009. Simple and complex interactions. In: Marine hard bottom communities: patterns, dynamics, diversity, and change (Vol. 206). Wahl, M. (Ed.), Springer-Verlag, Berlin, pp. 225-237.

Moriyasu, M., Landsburg, W., Wade, E., Maynard, D. 2000. The role of an estuary environment for regeneration of claws in the American lobster, *Homarus americanus* H. Milne Edwards, 1837 (Decapoda). Crustaceana, 72, 415-433.

Morrissey, E.M. 2016. Reproduction and recruitment of the American lobster (*Homarus americanus)* in the Great Bay Estuary, New Hampshire. M.Sc. Thesis, Department of Zoology, University of New Hampshire, Durham, N.H.

Munro, J., and Therriault, J.C. 1983. Migrations saisonnières du homard (*Homarus americanus*) entre la c ôte et les lagunes des Îles-de-la-Madeleine. Can. J. Fish. Aquat. Sci. 40, 905-918.

New Hampshire Fish and Game (NHFG). 2008. Monitoring of the American lobster (*Homarus americanus*) resource and fishery in New Hampshire. 20 p.

Oviatt, C.A. 2004. The changing ecology of temperate coastal waters during a warming trend. Estuaries. 27, 895-904.

Polis, G.A., Myers, C.A., Holt, R.D. 1989. The ecology and evolution of intraguild predation: Potential competitors that eat each other. Annu. Rev. Ecol. Syst. 20, 297-330.

Preisler, R.K., Wasson, K., Wolff, W.J., Tyrrell, M.C. 2009. in: Invasions of estuaries vs the adjacent open coast: a global perspective. Rilov, G., Crooks, J.A. (Eds.), Biological Invasions in Marine Ecosystems. 57 Ecological Studies 204, Springer-Verlag, Berlin, pp. 587-617.

PREP (Piscataqua Regional Estuaries Partnership). 2014. State of our estuaries 2013. University of New Hampshire, Durham, NH, 48 p. Available at: http://www.prep.unh.edu/resources/pdf/2013%20SOOE/SOOE_2013_FA2.pdf.

Richards, R.A., Cobb, J.S., Fogarty, M.J. 1983. Effects of behavioral interactions on the catchability of American lobster, *Homarus americanus*, and the two species of *Cancer* crabs. Fish. Bull. 81, 51-60.

Roman, J. 2006. Diluting the founder effect: cryptic invasions expand a marine invader’s range. Proc. R. Soc. B. 273, 2453-245.

Rossong, M.A., Williams, P.J., Comeau, M., Mitchell, S.C., Apaloo, J. 2006. Agonistic interactions between the invasive green crab, *Carcinus maenas* (Linnaeus) and juvenile American lobster, *Homarus americanus* (Milne Edwards). J. Exp. Mar. Biol. Ecol. 329, 281-288.

Rossong, M.A., Quijon, P.A., Williams, P.J., Snelgrove, P.V.R. 2011. Foraging and shelter behavior of juvenile American lobster (*Homarus americanus*): The influence of a non-indigenous crab. J. Exp. Mar. Biol. Ecol. 403, 75-80.

Ruiz, G.M., Carlton, J.T., Grosholz, E.D., Hines, A.H. 1997. Global invasions of marine and estuarine habitats by non-indigenous species: mechanism, extent, and consequences. Am. Zool. 37, 621-632.

Ruiz, G.M., Fofonoff, P., Hines, A.H. 1999. Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interaction. Limnol. Oceanogr. 44, 950-972.

Ruiz, G.M., Fofonoff, P.W., Carlton, J.T., Wonham, M.J., Hines, A.H. 2000. Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Ann. Rev. Ecol. Sys. 31, 481-531.

Short, F.T. 1992. The ecology of the Great Bay Estuary, New Hampshire and Maine: An estuarine profile and bibliography. NOAA – Coastal Ocean Program Publ. 222 p.

Short, F.T., Matso, K., Hoven, H.M., Whitten, J, Burdick, D.M., Short, C.A. 2001. Lobster use of eelgrass habitat in the Piscataqua River on the New Hampshire/Maine border, USA. Estuaries 24, 277-284.

Sigurdsson, G.M., Rochette, R. 2013. Predation by green crab and sand shrimp on settling and recently settled American lobster postlarvae. J. Crust. Biol. 33, 10-14.

Trowbridge, P. 2006. Environmental Indicator Report: Water Quality. New Hampshire Estuaries Project. 94 p.

Wahle, R.A. 1993. Recruitment to American lobster populations along an estuarine gradient. Estuaries. 16, 731-738.

Wasson, K., Fenn, K., Pearse, J. 2005. Habitat differences in marine invasions of central California. Biol. Inv. 7, 935-948.

Watson, W.H. III., Vetrovs, A., Howell, W.H. 1999. Lobster movements in an estuary. Mar. Biol. 134, 65-75.

Williams, P.J., Floyd, T.A., Rossong, M.A. 2006. Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and sub-adult American lobsters, *Homarus americanus* (Milne Edwards). J. Exp. Mar. Biol. Ecol. 329, 66-74.

Wolff, W.J. 1999. Exotic invaders of the meso-oligohaline zone of estuaries in the Netherlands: Why are there so many? Helgo Meersunters 52, 393-400.

Zar, J. H. 1999. Biostatistical analysis, 4th ed. Prentice Hall.

**Figure Captions**

**Fig. 1.** The Great Bay Estuary (GBE) in southeast New Hampshire and Maine. GBE encompasses three distinct areas: the Piscataqua River, Little Bay, and Great Bay. The location of our study sites are labeled 1-4, and correspond to a coastal-to-estuarine gradient: (1) Goat Island; (2) Fox Point; (3) Adams Point; (4) Nannie Island.

**Fig. 2.** Total catch by weight for cumulative subsamples of lobsters and crabs. (A) The weight-frequency relationship of green crabs ($n$ = 1229) and; (B) lobsters ($n$ = 142). Weight data were combined from 2013 and 2014. Many more green crabs were captured in Great Bay Estuary than lobsters (note the differences in the y axis parameters), and there was only a slight overlap between crabs and lobsters that weighed between 80 and 200 g.

**Fig. 3.** Length-Weight relationships for lobsters and crabs. Both relationships were fit using a power function. Length-weight relationships were extrapolated (asterisk markers) to include smaller lobsters to visualize the weight overlap that occurs between the two species. (A) fitted length data (2013) shows the predicted size frequency curve of lobsters ($n$ = 59), male green crabs ($n$ = 451) and female green crabs ($n$ = 365) captured and measured in GBE; (B) The same relationship was used to fit 2014 length data for lobster ($n$ = 85), male ($n$ = 162) and female green crabs ($n$ = 251). Regression equations are given in section 3.2.

**Fig. 4.** Catch-per-unit-effort (CPUE) for lobster (top) and green crab (bottom) in each of the two surveyed years. When comparing all of the sites in Little Bay (Goat Island and Fox Pont) to the sites in Great Bay (Adams Point and Nannie Island), there are significantly more lobsters in Little Bay during both years ($W$= 56.36, $P$ = <0.0001). During 2014 (but not in 2013), more green crabs were captured at Great Bay sites than in Little Bay ($W$ = 33.734, $P$ = 0.0001). Generally, there was a higher relative abundance of crab than lobster (note the difference in scale).

**Fig. 5**. Daily water temperatures at sites in Little Bay and Great Bay where traps were located in 2014. Water temperatures in Little Bay remained colder than Great Bay by about 2-3 $^{o}$C throughout the summer. The water temperatures during 2013 showed a similar profile, although conditions were generally colder in 2013.

**Tables**

**Table 1.** Size matrix of lobster-crab pairings for behavioral trials.

| | | Green Crab Weight (g) | | | | | |
|---|---|---|---|---|---|---|---|
| | | 0-20 | 21-40 | 41-60 | 61-80 | 81-100 | 100-120 |
| Lobster Weight (g) | 0-140 | 0 | 1 | 0 | 0 | 2 | 5 |
| | 141- 280 | 3 | 0 | 0 | 1 | 0 | 0 |
| | 281- 420 | 0 | 0 | 2 | 1 | 0 | 0 |
| | 421- 560 | 2 | 6 | 4 | 3 | 3 | 1 |
| | 561- 700 | 0 | 0 | 0 | 1 | 0 | 0 |
| | 701- 840 | 0 | 0 | 1 | 0 | 0 | 0 |

**Table 2**. Summary of lobster and green crab catch.

| | 2013 | | | 2014 | | |
|---|---|---|---|---|---|---|
| | Lobster | Green Crab (Male) | Green Crab (Female) | Lobster | Green Crab (Male) | Green Crab (Female) |
| n | 59 | 451 | 365 | 85 | 162 | 251 |
| Mean length (mm) ± SEM (observed) | 71.93 ± 1.52 | 68.56 ± 0.46 | 59.20 ± 0.45 | 69.52 ± 1.35 | 66.23 ± 0.57 | 61.63 ± 0.35 |
| Mean weight (g) ± SEM (predicted) | 314.37 ± 18.30 | 82.98 ± 1.33 | 50.11 ± 1.04 | 289.81 ± 16.13 | 74.41 ± 1.98 | 54.40 ± 0.91 |
| Mean CPUE ± SEM | 0.76 ± 0.15 | 3.69 ± 0.56 | | 0.27 ± 0.05 | 16.99 ± 2.50 | |

**Table 3.** Catch per unit effort (CPUE) of lobsters and crabs by year and region.

| | 2013 | | 2014 | |
|---|---|---|---|---|
| | Little Bay | Great Bay | Little Bay | Great Bay |
| Lobster | 0.39 ± 0.09 | 0.14 ± 0.05 | 1.52 ± 0.24 | 0.05 ± 0.03 |
| Green Crab | 20.03 ± 4.37 | 13.94 ± 2.41 | 0.59 ± 0.27 | 6.57 ± 0.71 |

Figure_1

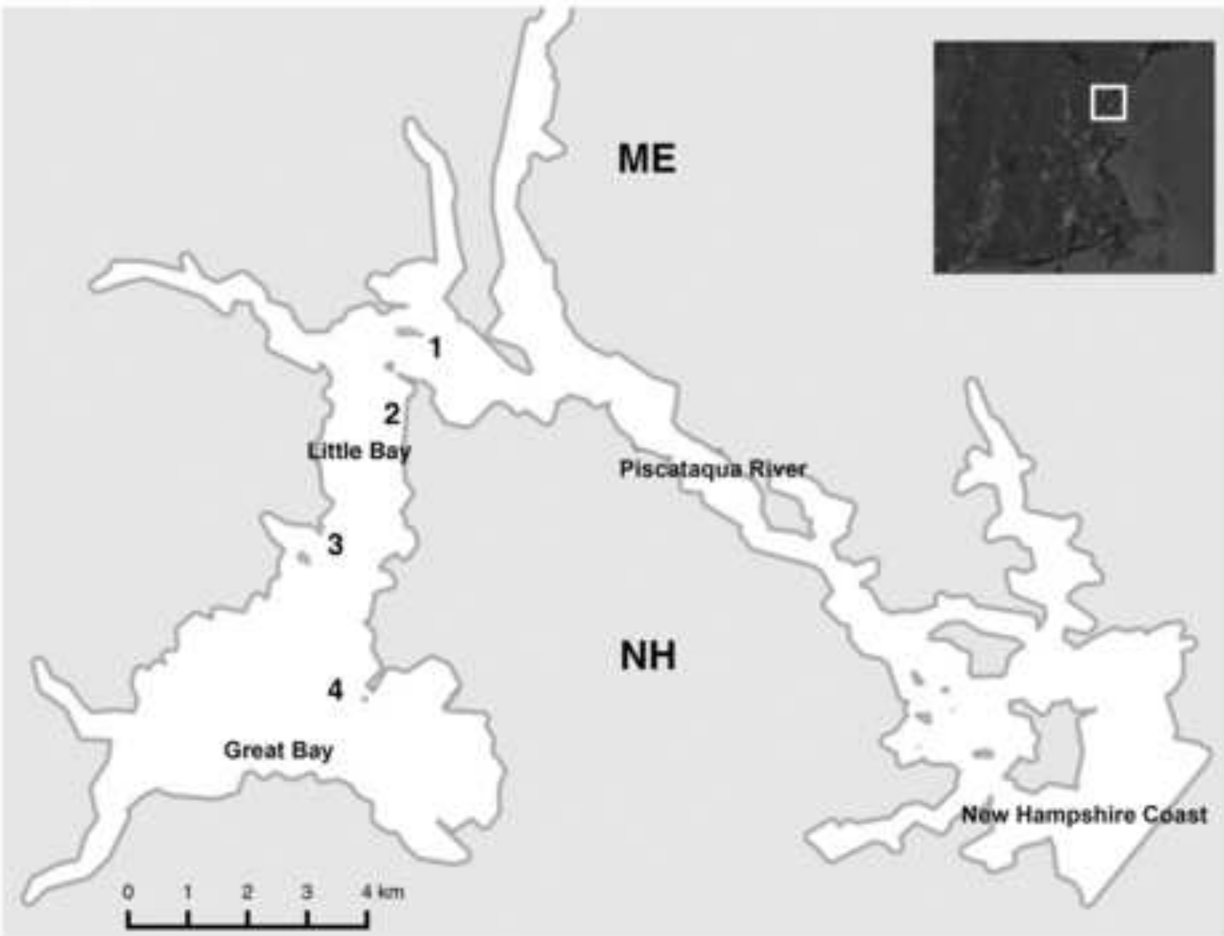

ME
1
2
Little Bay
Piscataqua River
3
NH
4
Great Bay
New Hampshire Coast
0
1
2
3
4 km

Figure_2

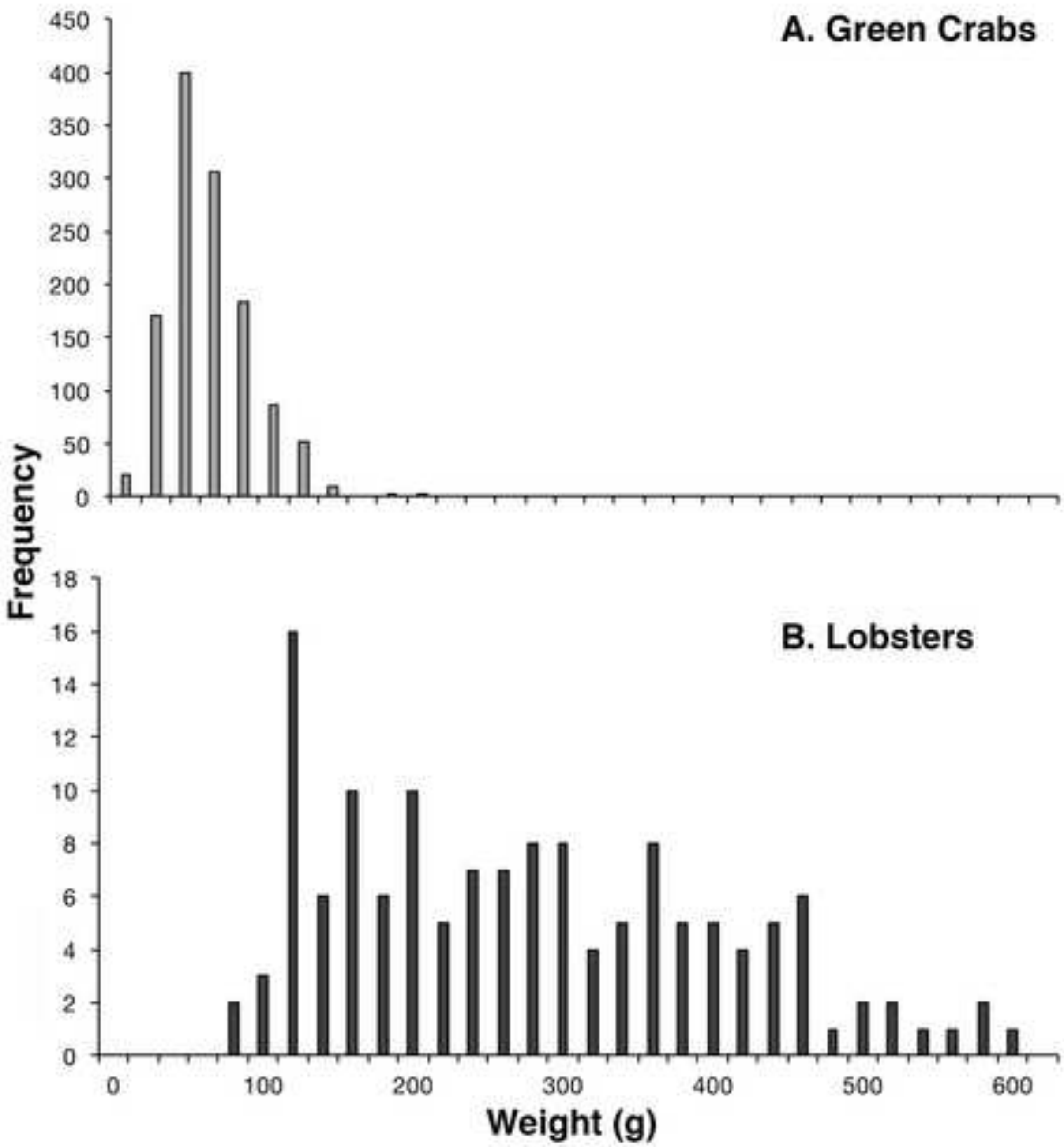
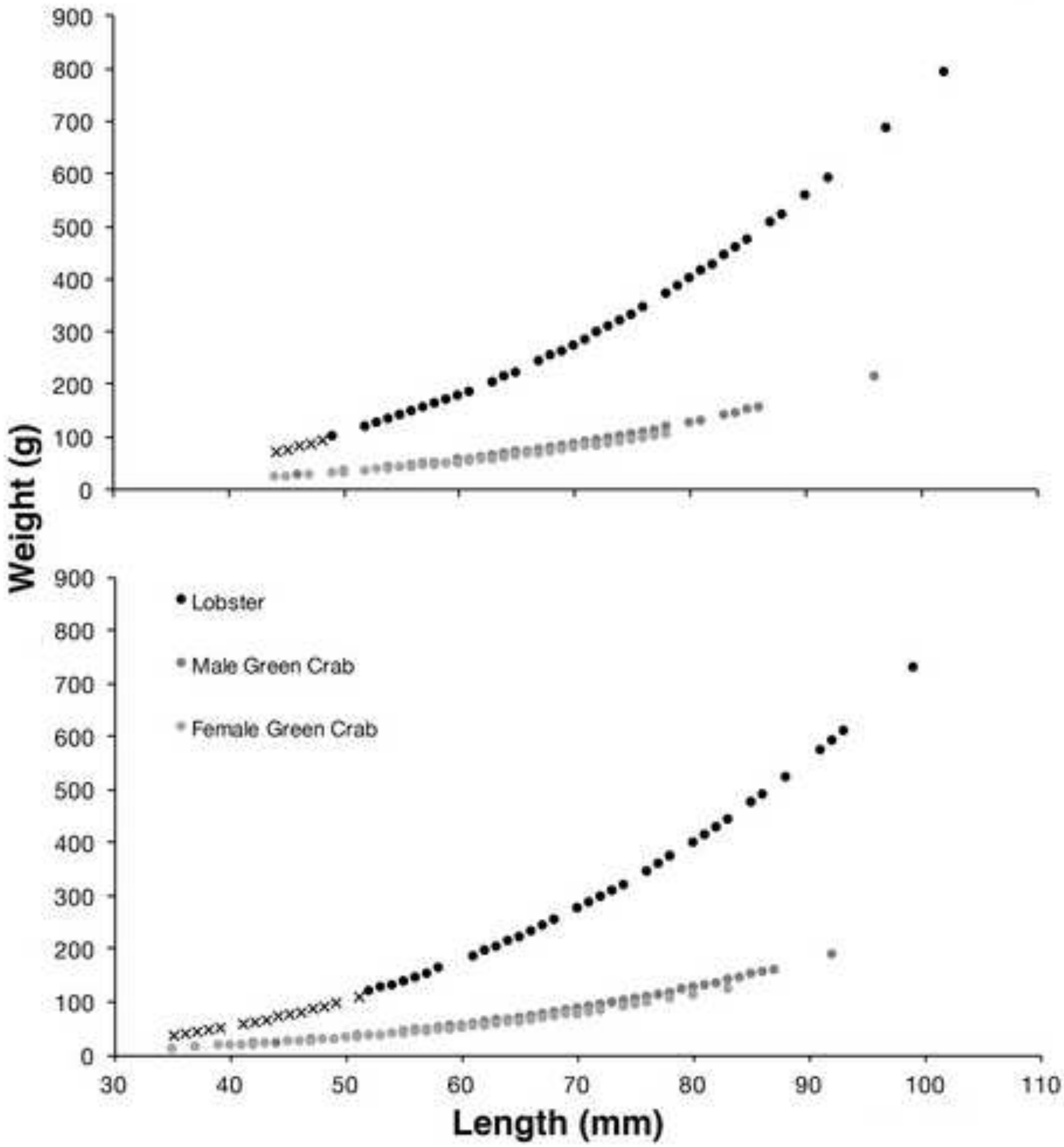

A. Green Crabs
B. Lobsters
Frequency
Weight (g)
450
400
350
300
250
200
150
100
50
0
18
16
14
12
10
8
6
4
2
0
0
100
200
300
400
500
600

Figure_3



900
800
700
600
500
400
300
200
100
0
Weight (g)
Lobster
Male Green Crab
Female Green Crab
30
40
50
60
70
80
90
100
110
Length (mm)

Figure_4

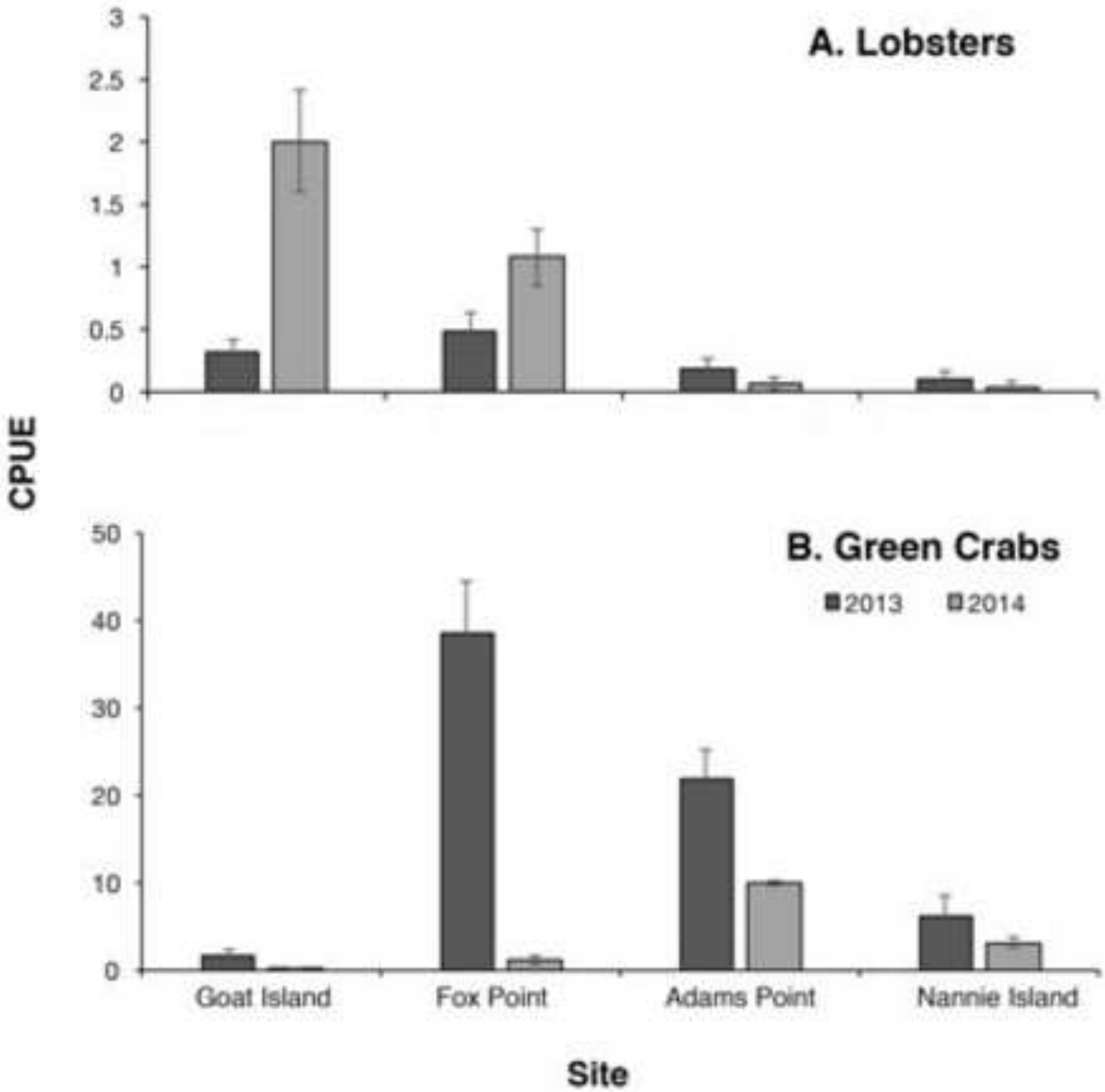
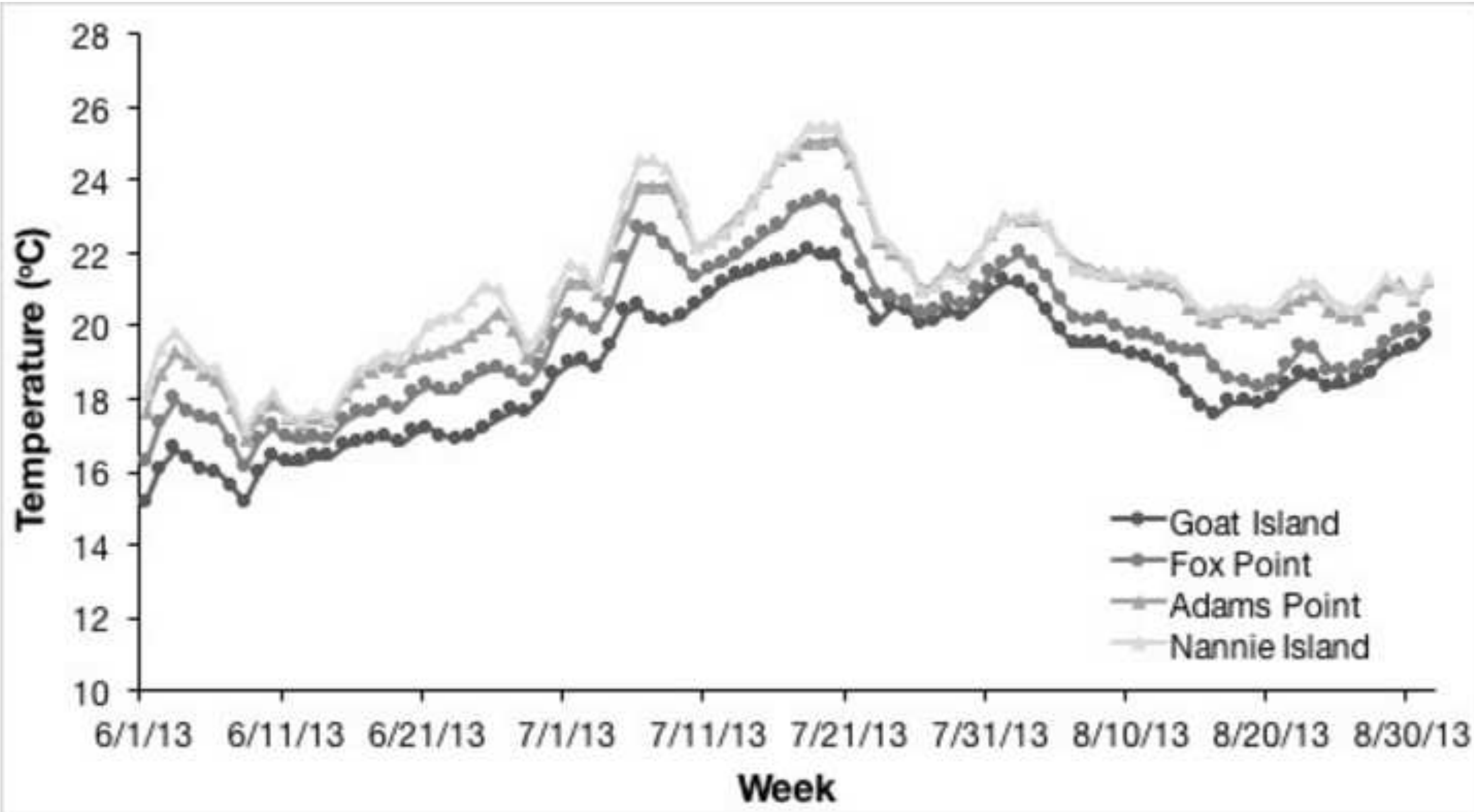

A. Lobsters
B. Green Crabs
2013
2014
CPUE
Site
Goat Island
Fox Point
Adams Point
Nannie Island
0
0.5
1
1.5
2
2.5
3
0
10
20
30
40
50

Figure_5



28
26
24
22
20
18
16
14
12
10
Temperature (ºC)
6/1/13
6/11/13
6/21/13
7/1/13
7/11/13
7/21/13
7/31/13
8/10/13
8/20/13
8/30/13
Week
Goat Island
Fox Point
Adams Point
Nannie Island