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The spatial and temporal distribution, population growth strategies and options for the removal of the invasive shore crab Carcinus maenas in two New Hampshire estuaries

Beth Allison Fulton

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Abstract
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Keywords
Biology, Zoology, Biology, Conservation, Biology, Ecology

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THE SPATIAL AND TEMPORAL DISTRIBUTION, POPULATION GROWTH STRATEGIES AND OPTIONS FOR THE REMOVAL OF THE INVASIVE SHORE CRAB *Carcinus maenas* IN TWO NEW HAMPSHIRE ESTUARIES

BY

Beth Allison Fulton

BS, Cornell University, 2009

THESIS

Submitted to the University of New Hampshire
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Professor of Biology and Marine Sciences and Zoology

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ABSTRACT

THE SPATIAL AND TEMPORAL DISTRIBUTION, POPULATION GROWTH STRATEGIES AND OPTIONS FOR THE REMOVAL OF THE INVASIVE SHORE CRAB Carcinus maenas IN TWO NEW HAMPSHIRE ESTUARIES

by

Beth Allison Fulton

University of New Hampshire, September, 2011

The spatial and temporal distribution of the green crab, Carcinus maenas, along with various green crab population parameters, were studied in two New Hampshire estuaries over a one-year period from November 2009 to October 2010. Results show that foraging activity in Great Bay Estuary peaked in December and March, and in HSE, in April and November. Crabs in both estuaries experienced synchronous breeding periods. Males experienced two molts per year in April and November, while females molted synchronously in June. Embryogenesis was accomplished within the month of June. Minimum size at maturity for females in New Hampshire was larger than the size at which maturity is attained by crabs in Maine and Canada. Trap saturation and escapement experiments were conducted in order to suggest modifications that could be made to experimental traps in order to increase catch per unit effort in future endeavors. A nutritional analysis of a homogenate of whole green crabs revealed that green crabs would likely make a suitable fishmeal substitute for ash tolerant species in aquaculture and agriculture.
INTRODUCTION

The European green crab *Carcinus maenas* is a pernicious invader that has plagued New England since the late nineteenth century. The green crab is euryhaline and eurythermal (Elner, 1980) and has a highly varied omnivorous diet, which has made it a model invasive organism for global dispersion in temperate areas (Carlton et al., 2003). To understand the economic and ecological impact of local green crab distributions, their relative spatial and temporal abundance must be examined, along with their strategies for reproduction and molting. These topics are discussed in Chapter 1 of this thesis. Chapter 2 evaluates the most efficient methods for green crab removal, and Chapter 3 discusses practical uses for these animals in reference to establishing a fishery.

**History of Green Crab Invasions; Ecology and Habitat**

The native habitat of *Carcinus maenas* follows the eastern coast of the Atlantic Ocean from Mauritania to Norway (Crothers, 1968; Roman and Palumni, 2004). The current invasive range of *C. maenas* (and *C. maenas/Carcinus aestuarii* hybrids) include temperate areas of Australia, Tasmania, South Africa, North America, and Japan (Carlton et al., 2003; Roman and Palumni, 2004). Dispersal of *C. maenas* by hull fouling and solid wet ballast began in the 1800s (Cohen et al., 1995), followed by a second wave of colonization coincident with the invention of faster methods of ocean travel and increased shipping in the mid-nineteenth century (Cohen et al., 1995). Larval dispersal by ballast water may have been possible (Hamer et al., 1998; Audet et al., 2003), as it has been
proven that planktonic larvae of *C. maenas* can survive up to 44 days at 12°C (Mohamedeen and Hartnoll, 1989). With the advent of air travel, a third wave of twentieth-century releases occurred by a variety of new mechanisms which included transport with (or as) aquarium materials and perishable fisheries products (Carlton et al., 2003). The green crab was first introduced to the eastern United States in 1817 via ports in New York and New Jersey (Welch, 1968). Green crabs had spread north to the vineyard sound in Massachusetts by 1873, and were observed in southern Maine (Casco Bay) in the 1890s (Carlton et al., 2003). By 1874, the southern limit of green crab invasion on the East coast of the United States was documented as having been established in Virginia (Kingsley, 1879). By the late 1990s and early 2000s, stable green crab populations had been documented as far north as the Bay of Fundy and Prince Edward Island in Nova Scotia (Carlton et al., 2003).

Many biotic factors have favored green crab invasion. The most notable of these are release from native parasites, absence of predators or competitor species, and the presence of favorable prey.

The release of the green crab from native parasites increases its invasive potential (Torchin et al., 2001). Native parasites of the green crab include the castrating rhizocephalan *Sacculina carcini* (up to 78% of native-range crabs infected), the egg-consuming nemertean *Carcinonemertes carcinophila* (up to 100% of native-range crabs infected), and certain trematodes of the *Microphalus* genus that behaviorally modify their intermediate green crab hosts (up to 100% of native-range crabs infected; Torchin et al., 2001). Increased parasitic prevalence in populations of green crabs has been associated with decreased crab size and increased limb loss (Torchin et al., 2001). Crabs infected by
certain parasites (e.g. rhizocephalans) do not molt, do not exhibit burying behaviors, and as a result are more likely to be fouled by epibiont communities, which may increase predation (Mouritsen and Jensen, 2006).

Absence of native predators favors an invading species like the green crab. In both its native and invasive tidal ranges, the green crab (especially in its larval and juvenile stages) has a variety of fish, bird, and mammalian predators (Crothers, 1968), but none of them are green crab specialists (Kuris et al, 2004). These predator-prey relationships are often life-stage dependent. For example, field and laboratory studies have demonstrated that the adult blue crab *Callinectes sapidus* preys on green crabs and even provides resistance to southward range expansion (DeRivera et al., 2005). However, green crabs also have been shown to outcompete juvenile blue crabs (*Callinectes sapidus*) for prime habitat and resources (MacDonald et al., 2007). Relationships like these are hard to quantify, but the presence of both species over an extended period of time suggests that neither species has a substantial advantage.

The most specialized predator of the green crab is man. A fishery for *C. maenas* as a delicacy for humans and as a scent for seafood-based products (Pascoal et al., 2009) occurs in Portugal, where the majority of captured crabs are exported alive to Spain. In 1997, the productivity of this fishery (together with a similar fishery in France) was estimated at 900 mt/year (Klassen and Locke, 2007). ‘Tiling’ for non-ovigerous crabs that are post-ecdysis (~10% of catch), and destined to be angling bait, is a small fishery in Britain (Sheehan, 2008). In the US, ovigerous crabs are favored as bait for channeled conch (*Busycon canaliculatum*) in MA, and for striped bass (*Morone saxatilis*) and tautog (*Tautoga onitis*) in NY. However, both the US and European fisheries are small-scale
Adult and juvenile *C. maenas* compete with a large suite of crustacean species for resources and habitat in their native European range (Hayward and Ryland, 1995). In New England, the number of similar crustacean species is much smaller (Pollock, 1998). A large volume of environmental research supports the hypothesis that exposure to a reduced number of competitors (also known as "reduced species richness") allows invasives (e.g. green crabs) a larger niche to occupy (Vermonden et al., 2010; Lanta and Lepš, 2008). *C. maenas*’ success in New England can be primarily attributed to its ability to fill open physiological and behavioral niches.

On the Atlantic coast of the US, *C. maenas* juveniles face competitive pressure from other exotics (e.g. the Asian shore crab, *Hemigrapsus sanguineus*; Jensen et al, 2002). However, the success of *H. sanguineus* juveniles is associated with the abundance of rocky intertidal habitat (McDermott, 1998; Gerard and Cerrato, 1999; Lohrer et al. 2000; Gilman and Grace, 2009), while juvenile *C. maenas* can subsist in areas of low structural complexity (Crothers, 1968; Amaral et al., 2009). In some estuaries, mudflats and sparsely vegetated areas may support the largest densities of the smallest *C. maenas* juveniles (Almeida et al., 2008; Amaral et al., 2009). *C. maenas* adults also are capable of tolerating lower salinities (Crothers, 1967) than *H. sanguineus* adults (Gerard and Cerrato, 1999). Once *C. maenas* reach adulthood, they favor shallow subtidal areas (<5.5m, Aagaard et al., 1995) probably as a refuge from their other major decapod competitor, *H. americanus* (League-Pike and Shulman, 2009; Lynch and Rémy, 2009). Interactions with other shallow subtidal crabs over food and shelter usually end in
C. maenas's favor (MacDonald et al., 2007); *C. maenas* employs a thick-shelled hunkering strategy for fending off attack and quickly acquires food and eats it where it lies, both of which are energetically more efficient than common competitors’ strategies (MacDonald et al., 2007).

The low crustacean species richness of New England relative to that of Europe, combined with *C. maenas*'s broad physiological and behavioral adaptability, indicates a continued future place for *C. maenas* in New England, even when assuming arrival of new invasive species.

*C. maenas* is a voracious omnivore, and new habitats must supply sources of nutrition for both larval and adult forms of the crab. Green crab larvae begin to feed in earnest after zoae stage 1 (Gimenez and Anger, 2005) rising to the water's surface in the evenings (Crothers, 1967) to selectively filter-feed on zooplankton, phytoplankton, protists (ie: dinoflagellates), and detritus (Hinz et al., 2001; Perez and Sulkin, 2003). Juvenile and adult crabs obtain nutrition from a variety of annelid, molluscan, arthropod, and finfish prey (Taylor, 2004) as well as from algal sources (Ropes, 1968). Molluscan prey, especially pelecypods, are a clear favorite among juveniles and adults (Ropes, 1968). Because *C. maenas* is primarily a soft flesh feeder with a simplified digestive system (foregut and hindgut; Crothers, 1966), analysis of *C. maenas* stomach contents is usually histological (Taylor, 2004, 2005; Feller, 2006). Due to the turbidity of its preferred living environment (mud flats), the primary mechanism by which *C. maenas* detects prey is via mechanoreceptors on its walking-leg joints and antennules and by chemoreceptors (funnel canals) on the surface of its legs, chelae, and mouth parts (Crothers, 1966; Waterman 1961). Therefore, juveniles and adults feed primarily at night
Carcinus maenas, like other native crabs of similar size (e.g. the rock crab, C. irroratus), exhibits a wide variety of feeding mechanisms including crushing, mandibular chipping, prying, and gape entry (Moody et al., 1992; Morton et al., 2008). These strategies make the green crab an efficient predator of bivalves even when feeding by crushing (the only method employed by larger Gulf of Maine conspecifics like H. americanus and C. borealis) is not possible (Moody et al., 1992).

**Abiotic Factors Favoring Green Crab Invasion**

The current invasive range of the green crab includes temperature extremes from the Gulf of St. Lawrence, Canada (where yearly bottom temperatures range from -2°C to 26°C with temperatures <10°C for 8 months of the year; Audet et al., 2003) to Japan (bottom water temperatures consistently around 25°C; Compton et al., 2010). Laboratory experiments indicate that adults have an upper thermal limit of 32°C (Cuculescu et al., 1998), which may be the primary preventer of southward invasion (Roman and Palumbi, 2004). The development of green crab larvae in laboratory settings is severely impeded outside of the 10-23°C range (Compton et al., 2010).

Adult green crabs are osmoregulators and can tolerate salinities from 35ppt down to 4ppt (Crothers, 1967; Cieluch et al., 2004) for prolonged periods of time without any adverse effects. Egg development requires salinities above 25ppt (Crothers, 1967; Anger et al., 1998). Generally, zoea instars, like protozoea, are osmoconformers (Cieluch et al., 2004) but osmoregulatory ability is present in megalopae and improves through adulthood with formation and development of posterior gill filaments (Cieluch et al., 2004).
It is known that green crabs cannot tolerate areas of high tidal energy (Compton et al., 2010) because the dactyls of C. maenas’s walking legs are poorly adapted to gripping rocky strata (Hampton and Griffiths, 2010). Adult green crabs cannot remain anchored on rocky strata in unidirectional flows faster than 0.23 m/s or when subject to vertical displacement forces greater than 3.64N (Hampton and Griffiths, 2010). Curved dactyls and thick dactyl spines would favor stability in high-energy intertidal environments, but C. maenas has straight dactyls, and fine, short dactyl spines (Hampton and Griffiths, 2010).

**Negative impact of C. maenas in New England**

The activity of C. maenas has negative economic and ecological impacts on a large set of native species in New England. In their foraging activities, green crabs bioturbate (uproot) natural and restored eelgrass (Zostera marina) beds, which provide an important refuge for juvenile fish and the larval forms of many species. Eelgrass prevents the erosion of mud flats by baffling wave action, and performs vital water-filtering functions (Davis et al, 1998). In the period between 1996 and 2004, eelgrass areal cover in the Great Bay Estuary in New Hampshire declined 17% (Short et al., 2008), and continues to decline (Short, unpublished). This estimate includes the 2.52ha planted by UNH researchers as part of a large local eelgrass restoration project (Short et al., 1997).

The impact of the presence of known eelgrass antagonists like the green crab relative to other effects like eelgrass wasting disease has not yet been investigated. However, in mesocosm experiments, green crabs at densities greater than 4 crabs/m² were able to bioturbate 40% of transplanted eelgrass shoots (Davis et al., 1998). Green crabs have been a major contributing factor to the decline of soft shell clam (Mya arenaria)
populations in New England (Welch, 1968) and are known to initiate predatory interactions with the quahog, *Mercenaria mercenaria* (Glude, 1954). In addition, green crabs destroy both natural and restored beds of young blue mussel (*Mytilus edulis*) (DeGraff and Tyrell, 2004) and Eastern oysters (*Crassostrea virginica*) (Miron et al, 2005). The US aquaculture yields of *Mercenaria mercenaria* and *Mytilus edulis* for 2007 were worth an estimated $67 million and $4.5 million, respectively (FAO, 2008). Green crab predation on blue mussels cultured in several of the most typical ways has been proven to be significant (up to six market-size mussels per crab per day; 10% of seeded individuals) and is a pernicious problem to the industry worldwide (Murray et al., 2007). Green crabs are also a significant predator of juvenile fishes (Fairchild et al, 2008), and may consume as much as 32% of the winter flounder year class in southern New England (Taylor, 2005). Trawls of the Hampton River, NH in 2004 revealed a 4-fold decrease in stocked winter flounder, (*Pseudopleuronectes americanus*), that coincided with a 7-fold increase in *C. maenas* population (Fairchild, 2009).

In experiments with adult *C. maenas* from Nova Scotia and juvenile American lobsters (*Homarus americanus*) from New Brunswick, Canada, it was found that green crabs were more efficient at locating and consuming food items than were juvenile lobsters, and adult crabs were very successful at defending food items from sub-adult lobsters (Rossong et al., 2006). Typically, green crabs respond to threats on food resources from other decapod crustaceans by simply turning their armored back on aggressors, while continuing to feed ravenously (MacDonald et al, 2007). Further, in laboratory studies, *C. maenas* is not only extremely successful in forcing juvenile lobsters from their burrows, but often causes lobster mortality in the process (Rossong et al.,
Experiments with adult *C. maenas* (55-75mm CW) and adult *H. americanus* (72-80mm CL) indicate that even in competition with adult lobsters, no significant differences in feeding time on a limited food resource were detected, and even though green crabs do not initiate agonistic encounters with feeding lobsters, 50% of those initiated by adult lobsters were lost to feeding green crabs (Williams et al., 2009). Extensive habitat overlap between green crabs and American lobsters in Canada has been confirmed by SCUBA survey (Lynch and Rochette, 2009) as well as in the US, including New Hampshire estuaries (Fairchild et al. 2008; see Chpt. 1).

**Life History of the Green Crab**

Most sources agree that crabs located from the Gulf Of Maine northward undergo one breeding period per season, which occurs sometime between the summer and the fall (Berrill, 1982; Audet et al., 2008). Environmental cues postulated for this phenomenon are temperature (Berrill, 1982; Queiroga et al., 1994; Audet et al., 2008), adequate nutritional state, and increasing day lengths (Crothers, 1967; Aiken, 1969). Before breeding, a molt is involved for females (Hartnoll, 1969) but not for males, who can mate continuously, contingent upon the possession of a hard shell at the time (Crothers, 1966; Audet et al, 2008). Female *C. maenas* do not possess reproductive opercula, which are a typical preclusion to hard-shelled mating in the Brachyura. However, unless recently molted, female *C. maenas* abdominal integuments are not sufficiently flexible to accommodate mating for mechanical reasons related to male pleopod structure (Spalding 1942; Hartnoll, 1968). Mature female *C. maenas* travel to breeding "hotspots" in estuaries prior to molt (van Der Meeren, 1994), and secrete uridine diphosphate (Bublitz et al., 2008) in their urine (Eales, 1974; Hayden et al., 2007), which is released at the
excretory canals at the base of the second antenna (Crothers, 1966). Uridine diphosphate is a sex pheromone that attracts males to premolt females and initiates male defense and “cradling” of prospective mates. Typically, males will undergo fights for rights to receptive females. Males with carapace widths >60mm are most successful, although males win the majority of conflicts if they are >9mm CW greater than their competitor (Reid et al., 1994). A successful male crab cradles his selected female right-side-up with some of his walking legs for about a week until the female is ready to molt (Bamber and Naylor, 1996; Bublitz et al., 2008). The female is released while she undergoes her molt (Hartnoll, 1969), and when she has finished, she turns over, extends her abdomen, and initiates clutching behavior on the male's ventral carapace with her walking legs while the copulatory styles of the male are inserted into her vagina (Spalding, 1942; Hartnoll, 1969). During this time, the hormone crustecdysone is released in the female's urine, which deters cannibalism by her mate (Eales, 1974; Hayden et al, 2007). The female then receives a spermatophore from the male that is stored in the spermatheca (a storage tube that branches off of the vagina) until internal fertilization takes place in the lumen of the ovary when it is ripe (Goudeau, 1982; Spalding, 1942). According to research conducted in Maine, fertilization is probably postponed for almost a year until the following late winter season (Berrill, 1982). Pre-extrusion, the female green crab carries 185,000 to 200,000 eggs internally (Cohen et al., 1995). After the female hardens, she is released by the male. Several months later, she will bury in the sand to extrude her eggs. Each egg is extruded individually and pressed with sufficient force against the setae to cause outer-membrane rupture, which ensures setae-adhesion (Crothers, 1967). The female's male partner, if he is "dominant" (about 5% of the male population), is free at this time to
breed with several more females in one season (van Der Meeren, 1994). The female will carry, clean, and prod her embryos with her setae for a period of approximately 3-5 months prior to protozoal release (Crothers, 1966; Audet et al., 2008; Vinuesa, 2005). In Maine estuarine and tidal areas, *C. maenas* protozoal release occurs in mid-to-late summer (Berrill, 1982). In Seabrook, New Hampshire, this release can begin anytime between April and July, according to first seasonal appearance of stage I zoae in 1978-1980 plankton data (Grabe, 2003). *Carcinus maenas* has one protozoal (embryonic, nonfeeding), four zoeal (planktotrophic, stage 1 nonfeeding), and one megalopal stage (Crothers, 1966; Rice et al., 1975; González-Gordillo et al., 2004). Typically, the protozoal stage lasts only hours, and green crabs complete all four zoal stages within a month (Berrill, 1982; González-Gordillo et al., 2004). Zoae IV morphs into a competent, settlement-cue responsive, megalopae that performs a series of diel, vertical, tidal, and ebb-tide migrations in order to move upstream in coastal waters where it will settle (González-Gordillo et al., 2004) by the end of summer (Berrill, 1982; Cameron and Metaxas, 2005). Juvenile crabs molt approximately 6-10 times in their first year to reach a CW between 4 and 25mm, depending on favorability of environmental conditions (Crothers, 1967; Breteler, 1975). Crabs reach maturity in 11-17 molts total (Breteler, 1975). On the mid- to southern coast of Maine, *C. maenas* matures at 2 to 3 years, and breeds 2 to 3 times thereafter, living approximately 6 to 7 years (Berrill, 1982). The process of molting is traumatic and has a large impact on a green crab's behavior in any phase of its life cycle. It is worth discussing the process of the molt in these animals to better understand molt staging as a tool for interpreting the survival strategy of this organism.
The Molt and Growth of C. Maenas

Molting in crustaceans is under endocrine control, mediated by a two-organ system of secretory cells. The Y-organ, a mass of cells located in the crab's maxilla, promotes molting by producing molting prohormones, also known as proecdysteroids (Crothers, 1967; Chung and Webster, 2003). These prohormones are converted to active ecdysteroids (hormones, e.g. 20-hydroxyecdysone) by cytochrome P-450 enzymes (Dam et al., 2006). The X-organ, which is located in the eyestalk of crabs, regulates the production of molt-inhibiting hormone (MIH). The transcription and titer of MIH does not change throughout the molt cycle of C. maenas, but the specificity of MIH binding in the Y-organ varies conspicuously (Chung and Webster, 2003). Increased binding of MIH in the Y-organ of crabs results in upregulation of cGMP and cAMP transcription, which causes downregulation of proecdysteroid production (Chung and Webster, 2003). Not surprisingly, eyestalk ablation (X-organ removal) is followed by hypertrophy of Y-organs and an immediate molt. Likewise, removal of the Y-organ results in molt inhibition (Knowles and Carlisle, 1956).

In order to understand the physical integumentary changes that occur during the molt cycle of C. maenas, a basic understanding of the structure of its integument is necessary.
Figure 1. Dorsally-located transverse section of a decapod crustacean integument during intermolt, adapted from Skinner (1962); Elofsson (1971); Noel (1983) and Roer and Dillaman (1984). 100x magnification. Cuticular thicknesses shown are for *C. maenas* in specific. Some epidermal structures may not be to scale. P= pore canal, I= integumental gland, R=reserve cell, B=blood sinus, C=chromatophore. In *C. maenas*, chromatophores are not present in the ventral integument.

The composition of the exoskeleton of decapod crustaceans is consistent across genera. The epicuticle consists of calcium salts and tanned lipoprotein; the exocuticle is a chitin-protein matrix impregnated with calcium-salt crystals (Roer and Dillaman, 1984). In *C. maenas*, the exocuticle (especially the ventral portion) also contains apoprotein-astaxanthin complexes that appear to provide photoprotection (Herring, 1972; 1973). The endocuticle is the thickest layer of the cuticle, comprising mostly chitin, with less protein inclusion in the matrix. This is the largest calcium reservoir of the exoskeleton. The membranous layer comprises protein and chitin but is not calcified (Roer and Dillaman, 1984). The epidermis is a metabolically active tissue that contains many different types of cells, including blood cells and reserve cells. In *C. maenas*, the dorsal carapace portion of this tissue also contains chromatophores closely associated with its basement membrane (Elofsson and Kauri, 1971; Elofsson and Hallberg, 1973; Noel,
These chromatophore cells are arranged in clusters (chromatosomes), and are under control of hormones (e.g. Red-Pigment Concentrating Hormone (RPCH), Pigment-Dispersing Hormone (PDH) and others; Rao, 2001). In the presence of these hormones, pigment granules move among and between chromatophores, along vast networks of microtubular arrays (Elofsson and Kauri, 1971; Elofsson and Hallberg, 1973; Noel, 1983). Juvenile green crabs can change their pigmentation in this way in response to the pigments of their background substrate, to day and night cues in which the crab becomes darker during the day and lighter during the night, and to temperature by becoming lighter in color as temperature increases (Crothers, 1968). These color changes can take between half an hour and several days, with time requirements increasing as carapace width increases. In adult crabs >35mm, chromatophores usually remain fully expanded at all times (Crothers, 1968). This phenomenon is probably related to the movement of juveniles out of the intertidal and into subtidal areas during adulthood. Chromatophores provide an excellent defense against visual- especially avian- predators (Todd et al., 2006).

The exoskeleton of crustaceans is also punctuated by pore channels that connect the epicuticle to the epidermis. These channels contain cytoplasmic material and are attributed with building and calcifying the exoskeleton of the crustacean (Skinner, 1962; Elofsson, 1971; Noel, 1983; Roer and Dillaman, 1984).

The molt cycle of *C. maenas*, and decapod crustaceans in general, consists of five discrete stages (and many sub-stages which are not discussed), as first described by Drach for *Cancer pagurus* (Drach, 1939). Among these stages, many physical and chemical changes occur in the cuticular layers and in the underlying epidermis. The
stages are A-B (Postmolt), C (Intermolt), D (Premolt), and E (Ecdysis, or the moment of the molt).

Stage D (Premolt) is characterized by all integumental layers having attained their final thickness and structure, and the membranous layer beginning to withdraw from the cuticle by apolysis, facilitated by proteolytic and chitinolytic enzymes (Skinner, 1962). This process begins in the appendages and works its way toward the core of the body. Fifteen to twenty percent of calcium from the old cuticle is resorbed by *C. maenas* through the pore canals during this period (Roer and Dillaman, 1984). New cuticular layers, epi- and exocuticle, are laid down under the apolysed region on top of the epidermis. In late premolt, crustacean cardioactive peptide (CCAP), a hormone that raises crustacean heart rate, is released from the pericardial organs into the haemolymph. This induces a raise in the crab's heart rate and increases the rate of scaphognathite beating, which raises haemolymph volume and pressure (Philippen et al., 2000). As a result, the crab begins to bloat with water.

Stage E (Ecdysis) is characterized by continued "water-drinking" (until maximum rate is reached) and an eventual rupture of the carapace. In the case of *C. maenas*, this occurs at the thoracoabdominal membrane, which is located at the junction of the carapace and the pleon. A green crab always walks backwards out of its discarded exoskeleton.

Stage A (Postmolt) is characterized by continued maximum rate of "water drinking" and scaphognathite beating, while the soft epi and exocuticle are inflated to create room for growth inside the new exoskeleton. Usual increases in size are about 1.1 to 1.3 times the size of the previously spent exoskeleton (Crothers, 1966; Breteler, 1975;
Berrill, 1982). Calcification of the epi- and exocuticles begins at the end of Stage A (about 10 hours post ecdysis) (Roer and Dillaman, 1984). During stage B (Postmolt), the endocuticle is deposited and additional calcification occurs.

Stage C (Intermolt) is the period during which the membranous layer is deposited. During this stage, the endocuticle is fully developed, and the volume (but not number) of epidermal cells increases (Roer and Dillaman, 1984). Dependent on the duration of this stage, an intermolt can be classified in one of two ways. If the crab concerned is young (not yet of reproductive size), and conditions are favorable for a brisk growth rate, the intermolt is termed "diecdysis". Diecdysis is usually a very short period, from which the crab immediately enters premolt (Knowles and Carlisle, 1954). When a crab is in diecdysis, many molts per season can be achieved. However, if the crab is of reproductive age and diverts energy to the production of gametes, or if conditions for growth are unfavorable, the animal can enter a longer intermolt stage, known as "anecdysis". When green crabs near the end of their life-cycle, they enter an intermolt phase called "terminal anecdysis" from which no further ecdyses take place (Crothers, 1967).

The length of a green crab's anecdysis can be identified by several anatomically-based methods including observation of setal changes on the expodites, development of limb buds, and the presence and extent of fouling organisms or black necrosis (Kaiser et al, 1990; Phlippen et al, 2000). However, a less intrusive and less time-consuming method is to observe the ventral color of the crab. Any individual green crab can express a large variety of ventral hues of varying saturation from blue-green to red. Recently
molten (postmolt) crabs are blue-green or green, but with increasing length of anecdyisis, they transition through yellow to orange to red (McGaw et al., 1992; Cheung, 1966).

As mentioned previously, during premolt, the epicuticle is laid down along with its photoprotective pigments. It has been noted that the carotenoid content and composition of crustacean exoskeleton does not significantly change over the course of a molt cycle (Castillo et al., 1987). Therefore, it is safe to assume that the same pigments laid down in the exocuticle during premolt remain in place until ecdysis.

The blue or green pigmentation of newly-molted crabs is associated with the presence of a large amount of a yet-unnamed polypeptide within the exocuticular matrix (weight approx 38,200d, \( \lambda_{\text{max}} = 625 \text{nm} \) consisting of a colorless apoprotein bound to astaxanthin (Garate et al., 1984). This protein can be loosely adsorbed with lutein, in which case the primary observed color will be yellow-green (Gilchrist and Lee, 1967; Garate et al., 1984). In the laboratory, in the presence of heat and gentle denaturing agents, this protein complex disassociates to astaxanthin \( (\lambda_{\text{max}} = 475 \text{nm}) \) and the colorless apoprotein (Garate et al., 1984). With near-complete denaturation, the primary observed color is red. It has been hypothesized that this apoprotein disassociates from its chromophore prosthetic group (asthaxanthin) in situ during a prolonged intermolt period due to photodenaturation (Cheesman et al., 1967). This hypothesis gains credence from the fact that carotenoproteins are known to be photoprotective in a large variety of marine and freshwater crustacean species (Herring, 1972; 1973).
Effect of Intermolt Duration on Dispersion, Anatomy, and Physiology

Once crabs attain sexual maturity, they spend more time between molts and therefore more time in anecydysis. Previous authors have termed these animals (during anecydysis) "red phase" crabs (Wolf, 1998; Lee et al., 2005). Their counterparts have been called "green phase" crabs. It follows that "red-phase" crabs are generally larger than their "green phase" counterparts (Hunter and Naylor, 1993).

So-called "red-phase" and "green-phase" crabs exhibit many other morphological disparities. Claw shell density and closer muscle are heavier in red-phase crabs, resulting in 28% greater crushing forces relative to green-phase crabs of the same size (Kaiser et al., 1990). Red-phase crabs also feed on larger mussels, are more likely to use slow-pulse forces for opening bivalves, and competitively exclude green-phase crabs of the same CW in laboratory settings (Kaiser et al., 1990). Red-phase crabs have thicker carapaces than green-phase crabs of the same size (McGaw et al., 1992), and are more successful than same-sized green-phase males in gaining access to receptive females (Styrishave et al., 2004). Green-phase (postmolt) crabs also generally have larger stores of fatty acid accumulated in their hepatopancreas than do red-phase crabs. This most likely is due to the mobilization of fatty acids to the crab's reproductive system for the production of gametes during anecydysis (Styrishave and Andersen, 2000).

Many physiological differences have been noted between so-called "red-phase" and "green-phase" crabs, including increased osmoregulation and oxyregulation capacity of "green-phase" crabs relative to "red-phase" crabs, (Reid et al., 1989; Reid and Aldrich, 1989). Although both morphotypes express endogenous circadian (nighttime activity) and
circatidal (high-tide activity) rhythms (Aagaard et al., 1995; Abello et al., 1997), green-phase crabs are more likely than red-phase crabs to express circatidal cycles, possibly because they spend less time in the subtidal and forage within the intertidal (McGaw and Naylor, 1992; Hunter and Naylor, 1993).

In crustacea, cytochrome P-450 enzymes convert ecdysone (a molting prohormone) to the hormone 20-hydroxyecdysone, which spurs ecdysis. However, the same enzymes also hydroxylate polycyclic aromatic hydrocarbons, making them water soluble and therefore excretable (Rewitz et al, 2003; Styrishave et al., 2004). Relative to red-phase crabs, green-phase crabs exhibit significantly higher P-450-family cytochrome gene expression in the presence of ecdysone (Rewitz et al., 2003). Red-phase crabs are less capable of metabolizing anthropogenic environmental pollutants (ie: polycyclic aromatic hydrocarbons) and, when faced with contamination, suffer higher mortality than green-phase crabs (Dam et al., 2006). Because of these physiological and morphological differences, the spatial and temporal distribution of crabs in anec dysis and diecdysis differs. Field research concerning the full spectrum of ventral colors expressed by green crabs in different habitats during all seasons is merited.
CHAPTER I

SPATIAL AND TEMPORAL ABUNDANCE OF THE GREEN CRAB IN TWO NEW HAMPSHIRE ESTUARIES

Introduction

Abundance of Green Crabs in New Hampshire

Green crabs are poikilotherms, therefore their metabolic rates are temperature-dependent (Elner 1980). Crab catch is highest during warmer months in estuaries (Glude 1954; Ropes 1969; Welch 1969; Flach 2003); green crab foraging activity is 15-20 times higher in summer and fall than in winter and spring (Aagaard et al. 1995). In New England, crab abundance reaches a maximum in the fall, and decreases with the onset of cold winter water temperatures as crabs migrate into deeper waters (Crothers, 1968). In milder winters, crab populations are able to flourish longer in shallow waters (Welch 1969; Dow 1972).

There are no published studies of green crab distribution and abundance in Great Bay Estuary (GBE) though green crabs are consistently present in seine surveys conducted by the NH Fish and Game Department (NHF&G; D. Grout, pers. comm.). In the Hampton-Seabrook Estuary (HSE), green crab abundance has increased substantially in the past 50 years. Surveys from 1954 to 1955 in Hampton Harbor, NH report catches of 35-155 crabs per sampling date using a modified scallop dredge (Ropes 1969). Since 1978,
Normandeau Environmental Associates Inc. (NAI) has gathered green crab abundance data in one area of the HSE using baited traps. General crab abundance oscillated from 1978 to 2006, but because of favorable climate changes, it is likely much higher than observed in 1969 (NAI 2005). In a 2008 trawl survey of the same area, green crab densities were as high as 0.2/m² (Fairchild et al. 2008b). However, crab abundance was likely underestimated, as sampling was done at low tide and during the day when green crabs are not as active (Ropes 1969), and was accomplished without bait. Crab density was much higher in another study when they were attracted (unintentionally) with live winter flounder, \( Pseudopleuronectes americanus \) in cages; crab density increased by over 600% in the presence of cages (Fairchild et al. 2008a).

Preliminary sampling to find low-predator areas in the HSE for winter flounder stock enhancement research indicated that there are areas, such as the Taylor River, where green crab density is much higher than in down-estuary areas (Fairchild, pers. obs.). It is evident from these studies and observations that a quantified green crab distribution and abundance study is merited in these highly prized estuarine systems.

**Local Projects Potentially Affected by the Presence of Green Crabs**

In recent years, the HSE has experienced a large reduction in \( M. arenaria \) recruitment due to mortality of juvenile life stages; 2010 juvenile stocks were at about 64% of their average level during the 1971-2000 interval (PREP, 2010). A 2002 manipulative field experiment in the HSE concluded that the majority of mortality in juvenile \( M. arenaria \) (resulting in low recruitment) in the HSE was attributed to predator density, rather than stocking density, neoplasia or environmental conditions (Beal,
Green crabs, in particular, were mentioned as a likely predator (Beal, 2002; NHEP, 2005; PREP, 2010). NAI has been conducting yearly density surveys for all *M. arenaria* life stages in the HSE since 1970 as part of the Seabrook Station Soft Shell Clam Monitoring Program. NAI lists the primary cause of predator-induced mortality in adult soft shell clams as human digging effort, but for young-of-the-year clams, predation by green crabs appears to be the primary cause, explaining 19% of variance (NAI, 2009). Other sources have estimated that green crabs can limit *M. arenaria* recruitment success by up to 80% (Flach, 2003). According to the Great Bay Restoration Compendium (Odell et al. 2006), soft-shell clams (*Mya arenaria*) are also a target restoration species in GBE, whose numbers may have been reduced in part by green crab predation. Further research has been suggested. Declining clam and flounder populations were also listed as problems in New Hampshire estuaries (Jones 2000); putative causes included predation. The 2010 Oyster Conservationist Final Report for GBE listed green crab predation on spat as a significant disruptor to oyster seeding efforts in the area (Ward et al., 2010). Further, recently-planted eelgrass in the GBE is often uprooted by the foraging activities of *C. maenas*, and planting the grass on a raised latticework does not help, as crabs also are attracted to structured habitat (Short, personal communication; Fairchild et al., 2008a). Surveys of green crab density over the course of an entire year in close proximity to these projects will more accurately indicate the extent of the impact of green crabs on these restoration and enhancement efforts. In addition, the relative density of green crabs in areas monitored concurrently by other projects may be indicative of ecosystem dynamics.
Goals of This Study

This study examined the abundance of green crabs at possible release sites for juvenile fish, stocking areas for eelgrass, seeding sites for oyster reefs, and locations of natural clam beds within the Great Bay Estuary (GBE) and Hampton-Seabrook Estuary (HSE) in an effort to inform future restoration efforts. The relationships between green crab distributions and several environmental variables, notably temperature and salinity, also were explored as a means of understanding local life strategies of these populations in reference to other regional populations. Reproductive and molt-stage data also were collected as part of this project.

No published studies have focused on quantifying subtidal green crab populations in the GBE and HSE, although extensive literature exists regarding green crab populations in Maine, Massachusetts, and Canada (Berrill, 1982; Able et al., 2002; McAneney et al., 2005; Cameron and Metaxas, 2005; Audet et al., 2008).

Methods

Study Sites

Green crabs were sampled in both the Great Bay Estuary (GBE) and the Hampton-Seabrook Estuary (HSE). In this study, the GBE includes the entire tidal basin (approximately 24.14 km in length) from the mouth of Portsmouth Harbor in New Castle, NH (shoreline habitat) to Dover and Newmarket, NH (estuarine habitat). The GBE has muddy, vegetated, and cobble bottom types, and includes approximately 3000 hectares of open water and marshlands (Brickner-Wood et al., 2006). Fed by eight rivers, the GBE has some of the strongest semidiurnal tides on the East Coast of North
America; current speeds in the Piscataqua River are as fast as 2.0 m/s (Swift and Brown, 1983). Tides in the GBE during sampling year 2010-11 varied from -0.13 to 2.85 m. Tidal lag from the mouth of the harbor to the most inland area of GBE sampled is approximately 2.4 h (Swift and Brown, 1983).

Locations of the sampling sites within the GBE are mapped on Figure 2. As shown, 12 sampling sites were chosen, labeled alphabetically A through L, with A as the site closest to the mouth of the estuary and L as the site farthest from the mouth of the estuary. Location coordinates, temperature tolerance, observed temperatures, salinity tolerance, observed salinities, depth range and bottom type for all locations are shown in Table 1.
Table 1. GBE site-specific information. Environmental data relating to site selection. Tolerance ranges indicate the ranges in which green crabs were caught, compared to total range of observed values. Information regarding bottom types in Portsmouth Harbor and GBE courtesy of Ward (1995), and Armstrong (1995). Sediment types were classified using the Wentworth sediment classification system.

<table>
<thead>
<tr>
<th>Site</th>
<th>Lat (d.d.)</th>
<th>Long (d.d.)</th>
<th>Temperature tolerance (°C)</th>
<th>Observed temperatures (°C)</th>
<th>Salinity tolerance (ppt)</th>
<th>Observed salinities (ppt)</th>
<th>Low Water Mark (m)</th>
<th>Bottom Type</th>
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<td>3-19</td>
<td>30-34</td>
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<td>Sandy</td>
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</table>
The HSE, located at the coastal border of New Hampshire and Massachusetts, is a temperate, shallow, sandy and muddy-bottom basin fed by five rivers and two smaller streams (Fairchild et al., 2008). Tides are semidiurnal, typically in the range between -0.35 and 3.15 m. The HSE’s main channels are subject to tidal sediment deposition and must be dredged approximately every five years by the U.S. Army Corps of Engineers. The HSE comprises approximately 1800 hectares of open water and marshlands (Eberhardt et al., 2009). Approximately 88% of the water in the estuary is turned over on each tide (Fairchild et al., 2008).
Locations of the sampling sites within the HSE are mapped on Figure 3. As shown, 14 sampling sites were chosen, labeled alphabetically M (the site closest to the mouth of the estuary) through Z (the site farthest from the mouth of the estuary).

Figure 3. Location of sampling sites in Hampton-Seabrook Estuary (HSE). Sites are labeled M through Z approximately according to distance from mouth of estuary. Sites M, P, Q, and U were sampled by NAI.
Location coordinates, temperature tolerance, observed temperatures, salinity tolerance, observed salinities, depth range and bottom type for each all locations within the HSE are shown in Table 2.
Table 2: HSE site-specific information. Environmental data relating to site selection. Tolerance ranges indicate the ranges in which green crabs were caught, compared to total range of observed values.

<table>
<thead>
<tr>
<th>Site</th>
<th>Lat (dd)</th>
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<th>Temperature tolerance (°C)</th>
<th>Observed temperatures (°C)</th>
<th>Salinity tolerance (ppt)</th>
<th>Observed salinities (ppt)</th>
<th>Low Water Mark (m)</th>
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<tr>
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<td>N/A</td>
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<td>29-33</td>
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<td>30-33</td>
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<td>15-33</td>
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</tbody>
</table>
**Trapping Study**

Twelve trap sites in the GBE (Figure 2) and ten sites in the HSE (Figure 3) were surveyed by subtidal trapping once monthly over a period of twelve months (November 2009 to October 2010). The remaining four sites in the HSE were surveyed twice monthly, in conjunction with the assessment of Seabrook Power Station by Normandeau Associates, Inc. (NAI) during the same time period. Trap site selection was made on the basis of establishing depth, bottom salinity, and bottom temperature gradients across both estuaries. Additionally, traps were placed in close proximity to former UNH restoration projects that may have been affected by the presence of green crabs. NAI sites were chosen based on proximity to oyster and mussel beds. The custom built crab traps were manufactured by Friendship Trap Co. to the same specifications as those used by NAI so trap data could be compared between UNH and NAI.

Results of the 2009-2010 NAI trapping studies within the HSE are incorporated into this study.
Traps were rectangular plastic-coated wire mesh measuring 61x28x31cm, with a single vertical chute in the top measuring 15x5x10cm deep. Trap lids were held shut with two 7cm corner-mounted pieces of flexible cord, and the traps were weighted (9 kg) and marked by buoys via 7-14 m of 23 kg-test rope. Video escapement experiments indicated that crabs may have been capable of escaping these traps, so traps were fitted with collars in Aug 2010. Later laboratory tests indicated no significant differences between funneled and non-funneled trap catches, therefore, no correction of catch numbers was necessary.

All trap sites were surveyed in duplicate, with a soak time of 24 hours. Variable fresh bait (monkfish, Atlantic salmon, cod, and salted herring) was used. All site-specific data (bait, bottom temperature, bottom type, soak time, latitude and longitude, depth, and bottom salinity) were recorded on each trip. Bottom water samples were obtained with a Niskin sampler for salinity (refractometer) and temperature (digital thermometer, Fischer Scientific). In later months (Sep-Oct 2010), a digital probe was used.
When hauled, the trap contents were sorted. All green crabs were bagged and brought to UNH where they were frozen until further analyses. All other species were identified, counted, measured, sexed (when possible), and released alive where captured. All crabs obtained via trapping were thawed, sexed, weighed (to the nearest 0.1 g), measured (carapace width, mm), and their color at sternite 5 was assessed visually and assigned a Value, Hue, and Chroma (V, H and C) corresponding with those of the Munsell paint color charts, 40 hue ed. (Munsell, 1950). Before visual color sampling was undertaken, all sample processors were tested for color blindness and were verified to have color acuity above the seventieth percentile according to the FM 100 Hue test, (an Xrite, Inc. product). Green crab eggs were staged visually as 1, orange (freshly extruded/yolky); 2, dark orange (less yolky); 3, red (medium maturity); 4, brown (medium to late maturity); or 5, black (late maturity/hardly yolky).

**Data Analysis**

Monthly CPUE was calculated for all sites in all months in the HSE and GBE. A one-way Kruskal Wallis ANOVA ($\alpha=0.05$) followed by Dunn’s nonparametric significance test of stepwise comparisons was used to determine which sites and which months constituted a significantly higher catch in each estuary.

Male and female CW and mass distributions across both estuaries were examined. Outlier crabs missing more than half a carapace or multiple limbs were discarded from the data set. Means of male and female mass and CW in each estuary (4 groups total) were compared by one-way between-S ANOVAs ($\alpha=0.05$) followed by Tukey’s’s HSD post-tests. All male and female crabs were grouped across estuary and all crabs from
HSE and GBE were grouped across sex. These groups were compared by one-way between-S ANOVAs ($\alpha=0.05$) followed by Tukey’s HSD post-tests as well.

The crab variables CW (mm) and mass (g) for males and females in each estuary were examined by scatter-plot in order to develop an allometric equation for the relationship between CW and mass for each of the 4 groups. The log of both variables was taken in order to linear-transform the data and the slopes of regression lines for males and females from each estuary were compared by ANCOVA with a Tukey’s HSD post-test. Females and males and HSE and GBE crabs were grouped into two datasets to determine allometric relationships across estuary and across sex. These data sets were fit with linear regressions, and were followed up by t-tests to determine differences between the two sets of slopes.

Expected relationships between environmental and crab (phenotype) variables were examined by the generation of scatterplots and crosstabs. A relationship in the HSE between bottom temperature and CPUE was explored by generation of a normally-distributed scatterplot, from which a mean and standard deviation could be calculated. Relationships between bottom type and CPUE for GBE were assessed by one-way-between-S ANOVA followed by a Tukey’s HSD post-test ($\alpha=0.05$).

One-way between-S ANOVAs followed by Tukey’s HSD post-tests ($\alpha=0.05$) were used to determine if mean V, H, and C measurements differed across sex or estuary. Linear regression analysis was conducted in order to determine any existing relationship between CW and distance from the mouth of the estuary and mean color values ($\alpha=0.05$).
An independent samples t-test (equal variances not assumed) was conducted to evaluate whether the salinity at which the largest CW (top 1SD) and smallest CW (bottom 1SD) of crabs captured were significantly different ($\alpha=0.05$). Amount of variance explained among V, H, and C values was tested through multiple regression ($\alpha=0.05$). Curvilinear and linear regressions were performed for V, C, and H against day length.

**Results**

**Green Crab Spatial and Temporal Distribution**

Poor weather prevented sampling in February in both estuaries and in the HSE in December. A trap site by Goat Island was tested from October through December of 2009 but was abandoned because no green crabs were ever caught there. Squamscott River (site L) was fished from May 2010 to October 2010; other months weren’t considered because of ice and prohibitively low temperatures. Traps were lost at site J (one trap) and K (both traps) in January, and at site H (one trap) in December, presumably because these traps were cut free of their lines by ice or were lost under the ice. One trap was lost at site G in August, one at site I in August, and one at site I in Oct. The buoys on these traps are presumed to have been weighed down by eelgrass and debris, rendering them irretrievable. Data from lost traps was not available, so the remaining trap was used in analyses for those sites and months.

Crab-yielding sample stations in the GBE experienced a mean salinity of 27.21ppt ($\theta=4.75$), with a low in April (21.48ppt) and a high in January (32.21ppt) (Figure 4). Crab-yielding stations in the HSE experienced a mean salinity of 31.78ppt ($\theta=2.30$), with
a low in November of 29.87ppt and a high in April of 34.26ppt. Mean bottom temperatures in the GBE and HSE were 12.99°C (σ=5.65) and 10.59°C (σ=3.23) respectively. HSE monthly means ranged from 17.41°C in June to 3.84°C in January. GBE took longer to reach mean maximum water temperature and stayed warmer longer, with a high of 21.74°C in July and a low of 3.90°C in January (Figure 4). Salinity and temperature fluctuations were greater in the GBE (Figure 4) than in the HSE. Salinity fluctuations in the GBE followed trends almost contrary to those seen in the HSE (Figure 4).

Figure 5. Bottom salinity and temperature in the GBE and HSE. These graphs display mean estuary-wide temperatures and salinities over time (±1SD). Day length (average for all monthly field days) is shown for purposes of considering water-heating delays. Only salinities and temperatures for sites at which crabs were captured are shown.

A number of species other than green crabs were attracted to the pots over the course of this field study (Table 3 and 4). The majority of these animals were dog whelk
(Nucella lapillus), but other species of crabs as well as juvenile lobsters and fish were captured. Trapping efforts in the HSE yielded less bycatch than efforts in the GBE.

Table 3. Total catch from the GBE

<table>
<thead>
<tr>
<th>Genus, species</th>
<th>Number caught</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carcinus maenas</td>
<td>2337</td>
</tr>
<tr>
<td>Nucella lapillus</td>
<td>2525</td>
</tr>
<tr>
<td>Cancer irroratus</td>
<td>412</td>
</tr>
<tr>
<td>Neopanopeua sayi</td>
<td>48</td>
</tr>
<tr>
<td>Cancer borealis</td>
<td>41</td>
</tr>
<tr>
<td>Rhithropanopus harrisii</td>
<td>36</td>
</tr>
<tr>
<td>Homarus americanus</td>
<td>29</td>
</tr>
<tr>
<td>Crangon crangon</td>
<td>16</td>
</tr>
<tr>
<td>Tautogolabrus adspersus</td>
<td>8</td>
</tr>
<tr>
<td>Pagurus sp.</td>
<td>5</td>
</tr>
<tr>
<td>Myoxocephalus scorpius</td>
<td>2</td>
</tr>
<tr>
<td>Anguilla rostrata</td>
<td>1</td>
</tr>
<tr>
<td>Crassostrea virginica</td>
<td>1</td>
</tr>
<tr>
<td>Fundulus sp.</td>
<td>1</td>
</tr>
<tr>
<td>Limulus polyphemus</td>
<td>1</td>
</tr>
</tbody>
</table>
Table 4. Total catch from the HSE

<table>
<thead>
<tr>
<th>Genus, species</th>
<th>Number caught</th>
</tr>
</thead>
<tbody>
<tr>
<td>Carcinus maenas</td>
<td>33721</td>
</tr>
<tr>
<td>Cancer irroratus</td>
<td>86</td>
</tr>
<tr>
<td>Cancer borealis</td>
<td>6</td>
</tr>
<tr>
<td>Asteroides sp</td>
<td>3</td>
</tr>
<tr>
<td>Nucella lapillus</td>
<td>2</td>
</tr>
<tr>
<td>Pagurus sp.</td>
<td>1</td>
</tr>
<tr>
<td>Rhithropanopus harrisii</td>
<td>1</td>
</tr>
<tr>
<td>Tautogolabrus adspersus</td>
<td>1</td>
</tr>
</tbody>
</table>

In the GBE, decapod crustacean species incidentally captured with green crabs shared much spatial and temporal overlap with green crabs, although there were a few notable exceptions. In the GBE, *N. sayi* were only found in August and September at sites G, J, and K. *R. harrisii* were only present in months June through October, and only in appreciable numbers (more than five animals per trap) at sites I-L. *H. americanus* juveniles were only captured in months April through November, and the majority of individuals (19 animals) were captured at sites A (4), B (8), and C (7). However, *H. americanus* were observed at all sites except L, with a decreasing presence as distance increased from the mouth of the estuary. *C. irroratus* were present year-round at all sites in GBE except L, where none were ever observed. Generally, *C. irroratus* were caught in higher numbers with increasing distance from the mouth of the estuary, with the exception of sites B and F and H, which had abnormally low catches, and sites C and G,
where a large numbers of *C. irroratus* were obtained. No *C. irroratus* were ever captured at site L. *C. borealis* were captured in similar numbers at sites A-J in all months except the December-March period.

In the HSE, site N caught approximately six times more *C. irroratus* total (57 crabs) than any other site. *C. borealis* was present April-October at sites N-Y, with a decreasing presence up-estuary. *R. harsii* were active in all areas of the HSE, but only during April-September, and no more than two crabs were captured at any site.
Figure 6: Average CPUE (crabs/hr) in the GBE. Error bars represent ±2 SEM.
Table 3. GBE average catch (average of duplicate traps, followed by sitewise and monthwise pooling of data) by site and by month. SEM and Tukey HSD homogeneous subsets (significantly different at or above the α=0.05 level) are shown. By month: F=205, df=10, p<0.001. By site: F=288, df=11, p<0.001.

<table>
<thead>
<tr>
<th>Month</th>
<th>Catch (avg)</th>
<th>SEM</th>
<th>Homogeneous subsets (α=0.05)</th>
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</thead>
<tbody>
<tr>
<td>Jan</td>
<td>7.31</td>
<td>0.57</td>
<td>a</td>
</tr>
<tr>
<td>Mar</td>
<td>63.33</td>
<td>2.20</td>
<td>i</td>
</tr>
<tr>
<td>Apr</td>
<td>19.89</td>
<td>0.70</td>
<td>d</td>
</tr>
<tr>
<td>May</td>
<td>12.65</td>
<td>0.84</td>
<td>c</td>
</tr>
<tr>
<td>Jun</td>
<td>18.88</td>
<td>1.13</td>
<td>d</td>
</tr>
<tr>
<td>Jul</td>
<td>27.80</td>
<td>0.88</td>
<td>f</td>
</tr>
<tr>
<td>Aug</td>
<td>11.89</td>
<td>0.45</td>
<td>b</td>
</tr>
<tr>
<td>Sep</td>
<td>21.53</td>
<td>0.69</td>
<td>e,f</td>
</tr>
<tr>
<td>Oct</td>
<td>30.91</td>
<td>1.03</td>
<td>g</td>
</tr>
<tr>
<td>Nov</td>
<td>20.48</td>
<td>0.53</td>
<td>e</td>
</tr>
<tr>
<td>Dec</td>
<td>59.32</td>
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<table>
<thead>
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<th>Catch (avg)</th>
<th>SEM</th>
<th>Homogeneous subsets (α=0.05)</th>
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<td>h</td>
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<tr>
<td>B</td>
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<td>0.45</td>
<td>a</td>
</tr>
<tr>
<td>C</td>
<td>3.79</td>
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<td>b</td>
</tr>
<tr>
<td>D</td>
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<td>f</td>
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<td>g</td>
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<td>G</td>
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<td>d</td>
</tr>
<tr>
<td>H</td>
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<td>i</td>
</tr>
<tr>
<td>I</td>
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<td>e</td>
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<tr>
<td>L</td>
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<td>0.00</td>
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Over the course of this one-year survey, 1,159 male and 1,178 female green crabs were removed from GBE. CPUE (crabs/hr) was highest in March, and lowest in January (Figure 5; Table 5) (p<0.001; df=10). With the exception of site L, which never yielded
any crabs, site B consistently produced the lowest catches and site F consistently yielded the highest catches (p<0.001; df=11). With the exception of site A (a high-catch site), CPUE of green crabs in the GBE increased with distance up-estuary through sites F, G, H, and I, and then began to decline with increasing distance up-estuary.

Figure 7: Average CPUE (crabs/hr) in the HSE. Error bars represent ±2 SEM.
Table 6. HSE average catch (average of duplicate traps, followed by sitewise and monthwise pooling of data) by site and by month. SEM and Tukey HSD homogeneous subsets (significantly different at or above the $\alpha=0.05$ level) are shown. By month: $F=5524$, df=9, $p<0.001$. By site: $F=1905$, df=13, $p<0.001$.

<table>
<thead>
<tr>
<th>Month</th>
<th>Catch (avg)</th>
<th>SEM</th>
<th>Tukey's HSD ($\alpha=0.05$)</th>
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</thead>
<tbody>
<tr>
<td>Jan</td>
<td>98.70</td>
<td>1.36</td>
<td>f</td>
</tr>
<tr>
<td>Mar</td>
<td>94.85</td>
<td>0.99</td>
<td>e</td>
</tr>
<tr>
<td>Apr</td>
<td>337.55</td>
<td>2.22</td>
<td>h</td>
</tr>
<tr>
<td>May</td>
<td>69.30</td>
<td>0.48</td>
<td>c</td>
</tr>
<tr>
<td>Jun</td>
<td>85.09</td>
<td>0.87</td>
<td>d</td>
</tr>
<tr>
<td>Jul</td>
<td>63.92</td>
<td>0.52</td>
<td>b</td>
</tr>
<tr>
<td>Aug</td>
<td>55.01</td>
<td>0.53</td>
<td>a</td>
</tr>
<tr>
<td>Sep</td>
<td>79.43</td>
<td>0.48</td>
<td>b</td>
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<tr>
<td>Oct</td>
<td>202.71</td>
<td>1.64</td>
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</tr>
<tr>
<td>Nov</td>
<td>533.38</td>
<td>2.41</td>
<td>i</td>
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</tbody>
</table>

<table>
<thead>
<tr>
<th>Site</th>
<th>Catch (avg)</th>
<th>SEM</th>
<th>Tukey's HSD ($\alpha=0.05$)</th>
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</thead>
<tbody>
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<td>N</td>
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<td>f,g</td>
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<tr>
<td>O</td>
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<td>d</td>
</tr>
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<td>P</td>
<td>61.08</td>
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<td>a</td>
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<tr>
<td>Q</td>
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<td>c</td>
</tr>
<tr>
<td>R</td>
<td>215.26</td>
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<td>e</td>
</tr>
<tr>
<td>S</td>
<td>101.08</td>
<td>1.08</td>
<td>d</td>
</tr>
<tr>
<td>T</td>
<td>518.93</td>
<td>5.28</td>
<td>k</td>
</tr>
<tr>
<td>U</td>
<td>56.76</td>
<td>0.28</td>
<td>a</td>
</tr>
<tr>
<td>V</td>
<td>321.35</td>
<td>4.38</td>
<td>g</td>
</tr>
<tr>
<td>W</td>
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<td>3.78</td>
<td>j</td>
</tr>
<tr>
<td>X</td>
<td>405.96</td>
<td>4.87</td>
<td>i</td>
</tr>
<tr>
<td>Y</td>
<td>284.18</td>
<td>3.39</td>
<td>f</td>
</tr>
<tr>
<td>Z</td>
<td>454.25</td>
<td>4.06</td>
<td>h</td>
</tr>
</tbody>
</table>

Over the course of this one-year survey, 11,491 male crabs and 23,230 female crabs were removed from HSE. In general, fishing efforts in the HSE were tenfold more
productive than those in the GBE. Catch peaked in November, with another catch spike in April (Figure 6; Table 6). CPUE was lowest in August (p<0.001). The most productive site in the HSE was T (Figure 6). In HSE, CPUE generally increased with distance traveled up-estuary.

In the HSE, CPUE was maximized at 11.8°C (Figure 7). No apparent association between CPUE and temperature was evident in the GBE crab data.

Figure 8. CPUE (crabs/hr) and bottom temperature in the HSE.
CPUE in the HSE and GBE were also maximized at 30 and 31 ppt (Figure 10), although a larger and more continuous salinity gradient was sampled in the GBE (Figure 4). No discernable relationship existed between CPUE and depth in either estuary.

In the GBE, CPUE decreased with increasing bottom sediment particle size (Figure 9).

Figure 9. CPUE (crabs/hr) (±1SEM) in the GBE as a function of bottom sediment type. Tukey's HSD significant differences (α=0.05, p<0.001, F=110, df=3) are represented by subset letters.
Sex ratio and the distribution of ovigerous females

Figure 10. Sex ratio expressed as percent female (±2 SEM) in the HSE and GBE by site (letter) and by month.
In both estuaries, sex ratio varied less over time than by site. The yearly average sex ratio (expressed as percent female) in the GBE was 48%. Sites C, I, A, and F were 64, 63, 56, and 54% female, respectively. Site J consistently had a 50% male-female sex percentage and all other sites were strongly male. Site B was the most male-dominated site (70% male). The standard error of the mean on these estimates is 0.20.

In the HSE, the yearly average sex ratio was 67%. Site R had the lowest percentage of females, 55%, on average, and site X had the highest percentage of males: 77%. The standard error of the mean on these estimates is 0.05.

If the average number of crabs captured is to be considered a measure of green crab foraging activity, in HSE, female feeding activity was maximized in the summer months as the sex ratio was skewed most toward females during this time. This trend was not as marked in GBE. In both estuaries, male feeding was high in April.
Figure 11. Sex ratio in the HSE and GBE along a salinity gradient. Note that only salinity values sampled in the field are displayed (the gradient is not continuous).

The greatest number of non-ovigerous female crabs was seen at salinities 30 and 31ppt in both estuaries, despite relative estuary-wide climate and sex ratio differences (Figure 10,11). In general, when salinity was <30ppt in the GBE, more males than females were captured. At salinities 27, 30, and 31ppt, more females than males were captured, and at salinities greater than 31ppt, male-skewed sex ratios again dominated. In the HSE, sex ratios remained consistent (~66% female) except at salinities 29, 30, and 31ppt, the latter two of which were extremely biased in favor of females.

In Great Bay, only two ovigerous females were captured during this study; one CW49, and one CW70, from site H (Oyster River) in July and site A (Little Harbor) in June, respectively. Both of these females presented orange (mid-stage) eggs. In the Hampton-Seabrook estuary, a total of 165 ovigerous crabs were captured. Although the majority (n=68) were captured in May, ovigerous crabs were trapped most months of the
year (Figure 12). The mean size of ovigerous crabs was 48 mm CW (N=55), with a
minimum of 36mm (N=2).

Figure 12: Female *C. maenas* fertility in the HSE, by month. The numbers of ovigerous
crabs are shown in boxes. Months for which no ovigerous females were found are not
included.

In the HSE, more ovigerous females (and a higher percentage of ovigerous
females relative to total females) were found closer to the mouth of the estuary.

However, this relationship only explained 26% of variance (Figure 13).
Figure 13. Relationship between the total number of ovigerous female green crabs captured at each site and their distance from the mouth of the estuary.

Ovigerous green crabs in the HSE were found along a portion of the sampled salinity gradient, but most were found at salinities closer to 33ppt (Figure 14). Salinities at which the highest numbers of females were caught were not the salinities at which the majority of ovigerous females were captured (Figure 14).
Figure 14. Number of ovigerous crabs captured along a salinity gradient.

Egg maturity in the HSE peaked in June (Figure 15). Eggs were present most months of the year and maturity was highly variable. When most ovigerous females were obtained, their egg stage was mid-to-late maturity.
Figure 15. Mean (±1 SEM) egg development stages from 1 (orange) through 5 (black) in the HSE. Sample size (N) is indicated within the bars. Months for which fewer than four eggs were staged are not included.

Molting schedule of crabs in the HSE and GBE

The ventral coloration of male and female green crabs in two estuaries was measured in order to determine the expressed ranges of Value, Hue, and Chroma, and to determine the associations among these variables within green crab integument as a
biological system. Value, Hue, and Chroma were all approximately normally distributed in males, females, and crabs from both estuaries (Table 7).

Table 7. Ranges and means for Value (V), Hue (H), and Chroma (C) in male and female crabs from both estuaries.

<table>
<thead>
<tr>
<th></th>
<th>GBE males</th>
<th>GBE females</th>
<th>HSE males</th>
<th>HSE females</th>
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<tr>
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<td>[4,9]</td>
<td>[4,10]</td>
<td>[2,9]</td>
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<tr>
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<td>0.04</td>
<td>0.01</td>
<td>0.01</td>
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<tr>
<td>0V</td>
<td>0.98</td>
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<td>1.11</td>
<td>1.19</td>
</tr>
<tr>
<td>N V</td>
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<td>1178</td>
<td>9226</td>
<td>18278</td>
</tr>
<tr>
<td>mean H</td>
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<td>8.55</td>
<td>8.60</td>
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</tr>
<tr>
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</tr>
<tr>
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Figure 16. Value, Chroma and Hue by sex and by estuary. Tukey’s HSD subsets are shown for each of the four groupings, males and females from each estuary (α=0.05, p<0.001)

Although the means of V, H, and C differed significantly across male, female, and HSE and GBE groups, these differences were on the magnitude of one unit, which would not represent a very large visual color difference, and may be attributed to human margin of error (Figure 16).

All three color variables were weakly correlated (R²=0.27, F=5359, p<0.001). As Hues decreased (became increasingly red), Chromas increased (the color became more saturated), and Values decreased (became less black or grey than white). The ventral coloration of male green crabs (expressed as Munsell V, H, and C) displayed clear temporal trends complementary to those expressed by females in each estuary. For males, the approaching molt (signified by peaks of bright, red color) happened in spring (April)
and fall (November) in both estuaries. For female green crabs, a single summer molt was accomplished in both estuaries (Figure 17).
Figure 17: Mean ventral color (±1SEM) of male and female green crabs in the HSE and the GBE over time. Munsell Value (V), Hue (H), and Chroma (C) are shown. Hue (right axis) ascends from red to yellow-green vertically. Chroma (left axis) ascends from 4 (white/washed out) to 12 (bright, pure, saturated color). Value (left axis, same scale) ascends from 4 (grey) to 12 (light grey/white). Times of prospective molt are denoted by arrows.
Figure 18. Carapace width compared to mean color (V, H, and C) values, arranged from smallest to largest crabs. When multiple crabs of the same size existed, means were used.

There was an extremely weak linear relationship between CW and all color parameters. The $R^2$ for CW and Value was 0.02, for CW and Chroma it was 0.04, and for CW and Hue, it was 0.02 ($p<0.001$ for all three regressions). The synchronous ventral color change in females appeared to be most strongly correlated with day length; correlations with bottom temperature were weaker, because bottom temperature followed a different temporal trend with different maxima and minima in each estuary.
Figure 19. Female green crab ventral coloration correlated with day length. Error bars are ±1 SEM. Chroma ascends the right axis from faded to saturated. Hue moves vertically along the left axis from blue-green (5GY) to red (10R). ANOVA for these associations had p<0.001.
\[ C, \quad y = 0.4413x + 1.948 \quad R^2 = 0.841 \]

\[ H, \quad y = 0.5319x + 9.1997 \quad R^2 = 0.7595 \]
Value was negatively correlated with day length, and the relationship was weaker ($R^2 = 0.34$, $p<0.001$).

**Green Crab Mass-For-Width Relationships**

Size distributions of male and female crabs in the GBE and HSE were normal. Average male and female CW in the GBE were 60.40mm ($\theta=10.52$, $N=1159$) and 55.15mm CW ($\theta=7.51$, $N=1178$), respectively. Average male and female masses in the GBE were 54.56g ($\theta=27.34$, $N=1159$) and 38.30g ($\theta=15.23$, $N=1178$), respectively. In the HSE, average male and female masses were 38.73g ($\theta=15.70$, $N=9224$) and 29.41g ($\theta=8.67$, $N=18274$), respectively. Average male and female carapace widths in the HSE were 55.12mm ($\theta=7.25$, $N=9225$) and 50.96mm ($\theta=5.32$, $N=18247$), respectively. Comparisons between sex and estuary for these means showed all groups to be significantly different from each other, except for males from HSE and females from GBE, (Figure 22)(CW ANOVA $F=1534$, df=3, $p<0.001$) (Mass ANOVA $F=2272$, df=3, $p<0.001$).
Figure 20. Mean mass (g) and CW (mm) for male and female crabs in the HSE and GBE. Error bars are ±1 SEM. Different letters indicate significant differences (p<0.001) between means, (α=0.05).

Grouped across estuary, on average males (mean CW =55.71, mass= 40.5, SEM=0.07 and 0.18) were larger than females (mean CW =51.22, mass= 29.95, SEM=0.04 and 0.07) (p<0.001). Grouped across sex, green crabs in the GBE (mean CW
=57.75, mass= 46.36, SEM=0.20 and 0.49) were significantly larger than green crabs in
the HSE (mean CW =52.36, mass= 32.54, SEM=0.04 and 0.07) (p<0.001).

Scatter plots of CW (x) and mass (y) revealed that in all cases these variables
were related by an equation of the form mass (g) = k(CW(mm))^b. ANCOVA revealed that
all regression slopes were significantly different (p<0.001) (Figure 21). Log-log
transformation of the raw data yielded straight lines.
Figure 21. Regression lines for all four subsets of crabs (HSE and GBE, male and female). Regression lines for cross-estuary grouped sex and cross-sex grouped estuary are not shown, but their equations are listed in this figure.

Similarly, slopes relating all males to all females and relating all HSE crabs to all GBE crabs were significantly different (p<0.001). The fact that all of these mass-for-width curves intersect within the observed size range of crabs indicates that no one group maintains a mass-for-size increase over all other groups at all points within the observed range.
The largest crabs captured (top 1SD, CW>66, N=202) were consistently captured at higher salinities (mean=29.85ppt, SEM=0.970) than the smallest crabs (bottom 1SD, CW<40mm, N=26) captured (mean=27.38, SEM=0.298) (independent samples t-test, equal variances not assumed, p=0.02).

**Discussion**

Relative species diversity within the GBE was higher than it was in the HSE, and catch of species other than green crabs constituted a higher proportion of total catch in the GBE than it did in the HSE. This phenomenon is probably partially explained by the more diverse habitat options available in Great Bay Estuary, which comprises salt marsh, mudflat, deep channel bottom, eelgrass bed, and rocky intertidal habitats (Armstrong, 1997). The HSE is a much more simple system, comprising mud flats, shallow sandy bottom, and salt marsh, which may not provide all of the requirements to support a larger species diversity (Fairchild et al., 2008).

The lower catch of green crabs in the GBE relative to the HSE may be due to the higher species richness (diversity) of the GBE. The larger number of competitor and large predator species in the GBE may decrease the species niche available to green crabs in the GBE.

Many other species of benthic crustacea were attracted to green crab traps, and their degree of spatial overlap with green crabs provides insight into possible interactions among these communities. Mud crabs, American lobsters, and rock crabs have been listed as potential green crab competitors and therefore are of special interest (Audet et al., 2003). In the GBE, *R. harrisii* and *N. sayi* populations appeared to be found almost
exclusively farther up-estuary than the bulk of green crabs. Like *C. maenas*, *R. harrisii* and *N. sayi* are also osmoregulators, but are small species, relative to the green crab, and are therefore expected to be better volume regulators (less stenohaline). This may allow them to inhabit habitats farther up-river than green crabs, thus avoiding antagonistic interactions with *C. maenas* (Thomas and Rice, 1992; Davenport, 1972). The bulk of captured *H. americanus*, however, were present closer to the mouth of the harbor than most *C. maenas*. This effect was most likely due to the fact that *H. americanus* are limited osmoregulators, and juveniles who molt frequently are especially sensitive to osmotic stresses (Watson and Howell, 1999). *C. irroratus* were found to have a spatial distribution similar to that of *C. maenas*, but sites that yielded the largest numbers of *C. irroratus* did not yield relatively large numbers of green crabs. The relative exclusion of green crabs from pots with many *C. irroratus* or in traps including *H. americanus* is tested for statistical significance in Chapter 2 of this thesis (trap considerations).

The relative spatial and temporal abundance of flatfish in GBE and HSE examined in previous studies may also partially explain the spatial and temporal green crab abundances discovered by this study. Winter flounder, *Pseudopleuronectes americanus*, primarily use GBE as a nursery grounds, with the majority of fish caught in the estuary being $0^+ 1^+ 2^+$ individuals (Armstrong, 1995). Sites C (Back Channel) and H (Oyster River) sampled in this study were proximate to sites 1 and 3 sampled by Fairchild et al. in 2000 as possible release sites for juvenile winter flounder. However, winter flounder abundance at both of these sites was low and showed no statistically significant difference between sites and the same was true of green crab abundance (Fairchild, 2002).
In studies conducted by Armstrong (1997; 1995), otter trawls were used to estimate the abundance of winter and smooth flounder *Pseudopleuronectes americanus* and *Pleuronectes putnami* at several sites in the GBE, including ones proximate to site L and site J discussed in this study. At the site near site J, months of highest smooth flounder abundance were May and June and winter flounder were present in greatest numbers in May, although their numbers were fairly consistent throughout the year. Green crab mating activity in GBE peaks in June (probably corresponding with reduced feeding activity, which explains lower CPUE), so it may be an advantageous time for flounder to be more active during this time in areas where green crabs are usually present. In addition, site L (where no green crabs were found in this study) was the site of greatest abundance of smooth flounder. Winter flounder were also present at this site, but only in summer and early autumn because of salinity constraints (Armstrong, 1995).

In 2004, Fairchild et al. conducted a study in the HSE in which green crab and winter flounder densities were examined by beam and otter trawls at locations roughly proximate to sites S, T, V, W, and X sampled in this study. In both beam and otter trawls, sites of green crab abundance listed from most abundant to least abundant in both types of trawls were T, X, W, V, and S. The results of this study also list these sites (on average) from most abundant to least abundant as T, X, W, V, and S. This result demonstrates two findings: 1) green crab abundance in these areas of HSE is probably fairly consistent over time (which would facilitate removal) and 2) the null hypothesis that CPUE in this study’s traps is an accurate representation of spatial abundance is probably sound. Generally speaking, sites with higher green crab catches caught lower
numbers of winter flounder, but this correlation was weak and did not come close to fully explaining winter flounder distribution (Fairchild et al., 2008).

It may be that smooth and winter flounder slightly alter their spatial and temporal location based on the presence of green crabs, but primary influences are probably many other factors, especially salinity. It is also possible that the reduced presence of smooth and winter flounder in highest times and areas of green crab catch is simply the result of increased predation.

Increasing presence of green crabs with distance up-estuary is common in estuarine systems worldwide, with green crabs being one of the most osmotically-tolerant crab species in most estuaries (Mathieson and Berry, 1997). However, in cases when a larger salinity gradient in a strongly-tidal area is sampled, maximal CPUE can sometimes be obtained toward the middle of an estuarine salinity gradient (Rewitz et al., 2004).

In the GBE, CPUE was maximized mid-estuary, while this was not the case in the HSE. The probable reason for this result is that a larger salinity gradient was sampled in GBE. If the same salinity gradient had been sampled in HSE, a reduction in CPUE further up-estuary may have been detected. In GBE, it is possible that site L constituted a salinity barrier to green crab migration further upriver, as no green crabs were ever caught there. CPUE maximization at 30 and 31 ppt in both estuaries was the result of a large turnout of females. A large catch of females have been observed in the areas of estuaries with medium salinities by other researchers as well (Abello et al., 1997). This is probably due to the fact that female green crabs have a shorter foraging range than male crabs, and months of the year must be spent close to breeding hotspots and areas close to
the mouth of the estuary where egg incubation is optimized. (Cameron and Metaxas, 2005).

In GBE, CPUE increased with decreasing sediment particle size. This could be an indicator that there are more crabs on softer substrates or that crabs on softer substrate exhibit more pronounced feeding responses. A positive association between decreased particle size and increased catch per unit effort may be spurious, due to the presence of other favorable environmental variables associated with mud in the GBE (e.g. eelgrass) or with smaller particle size in general. Smaller particles are washed away in areas of higher flow, and large-particle sediments like pebbles and cobble are left behind. As mentioned previously, green crabs do not possess the necessary dactyl structure for gripping these types of strata in high-current areas. This relationship between bottom-type and CPUE may also be a statistical anomaly, as green crabs are known to be highly mobile animals. To test these preliminary hypotheses, a more continuous gradient of all substrate types in the GBE should be tested in future studies. Further research regarding this result, including core samples taken in the exact areas to be trapped, is merited.

As mentioned earlier, good habitats for green crabs are characterized by tolerable flow rates, the presence of sheltering structures, food resources, and the absence of competitors and large predators. In GBE, the mouths of tributaries branching off the middle of the bay provided many of these features, including small particle size, lower current speed, sheltering structure in the form of clam beds, oyster reefs, and eelgrass beds, and prey in the form of shellfish assemblages and flatfish which, like green crabs, prefer smaller particle sizes, which facilitate burying.
In the HSE, CPUE was maximized at bottom temperature of 11.8°C. Putative explanations for this phenomenon include the idea that green crabs, as poikilotherms, have an optimal metabolic operating temperature range, at which mobility will be at its maximum (Summich and Morrissey, 2004). In addition, temperature might act as an activating cue that spurs mobility of these animals at times of the year when available calories outweigh the cost of those spent acquiring them (Audet et al., 2008). For example, intertidal green crab locomotion markedly increases when temperatures rise above 7 or 8°C (Ropes, 1968; Rasmussen, 1973; Berrill, 1982; Aagaard et al., 1995). Green crab foraging may reach its maximum in the spring and fall because crabs are recovering from and preparing for an extended winter fast (Styrishave and Andersen, 2000). Additionally, when the water reaches maximum temperatures, green crabs may be seeking mates and therefore have little interest in feeding (Crothers, 1967). In addition, UV exposure may be a risk for these animals, especially those migrating on the shallow mud flats.

Migration of crabs to deeper, more saline environments during the colder months of the year as documented in previous studies (Naylor, 1962.; Rasmussen, 1973) was not observed, most likely because depths sampled did not constitute the full migration range of the green crab. This is consistent with the findings of previous literature that sampled similar subtidal depths (Rewitz et al., 2004). The full extent of subtidal green crab travel and migration is not known at this point in time (Styrishave and Andersen, 2000).

Sex ratios in both GBE and HSE were both consistently within 0.2 of the expected 1:1 ratio (Rewitz et al., 2004). Different operational sex ratios in the HSE and GBE could have been a sampling artifact caused by sampling different salinity gradients.
in each estuary. If more sites of median salinity (around 30 and 31 ppt) had been sampled in GBE, it is likely that more females would have been captured. The sex ratios of green crabs in both the HSE and GBE did follow some of the marked temporal trends, that have been noted in previous studies. Reduced male feeding activity during the summer, which was noted by Hayden et al. (2007) was observed most clearly in the HSE. As will be discussed shortly, on a temporal basis, sex ratios were usually skewed towards the sex that had just completed a molt (when feeding activity and growth would be expected to be most pronounced).

No significant relationship was seen between tide height and observed sex ratio, most likely due to the fact that this sampling regime was entirely subtidal, and males would be more likely to be found foraging at high tide in shallower depths than those sampled in this study (Rewitz et al., 2004).

The number of females captured appeared to be affected by salinity and distance from the mouth of the estuary: non-overgious females appeared to prefer moderate salinities 27-31ppt (and travelled further inland to find them), whereas berried females preferred relatively higher salinities, closer to the mouth of the estuary, around 33ppt. This pattern of behavior has been noted in previous literature and has been attributed to the smaller foraging range of female green crabs, relative to males, and the increased survival of incubated eggs at higher salinities (Cameron and Metaxas, 2005). The number of berried females captured, at maximum, 0.8% of the total female population, is almost certainly an underestimation of the overall abundance of ovigerous females, because females carrying eggs are known to remain buried in sediment for long periods and to feed only intermittently (Cameron and Metaxas, 2005). Unbaited trawl studies have
documented tenfold more ovigerous green crabs in estuarine systems (7.5%), (Mathieson and Berry, 1997).

Although a relationship was found between salinity and the number of ovigerous females caught, no linear or curvilinear associations existed between CW and temp or CW and salinity. This lack of association is probably explained by the fact that green crabs are so mobile. In a tagging experiment conducted in the Ria de Aveiro lagoon in Portugal, within one calendar year 65.8% of recaptured tagged green crabs moved 1-5 km and almost a quarter of recaptured tagged green crabs moved 5-10 km from their original release location (Gomes, 1991). However, the largest crabs captured (top SD of overall population) were consistently captured at much higher salinities than the smallest crabs captured (bottom SD of overall population). This statistically significant finding is replicated in the literature (Crothers, 1968).

The minimum reproductive size of female green crabs in Maine, USA has been reported as 34 mm CW (Berrill, 1982) and 28.66 mm in the Gulf of St. Lawrence, Canada (Audet et al., 2008). The results of our study indicate that female crabs in New Hampshire mature at 36 mm CW. This data is consistent with the observation made by Berrill that invasive crustaceans reach reproductive size at a smaller size with northward range expansion (Berrill, 1982).

Many studies have quantified green crab molting (and, by association, mating) periods by referencing crab ventral coloration. Usually, designations were arbitrarily made in designating crabs as "red-phase" or "green-phase" (Audet et al., 2008; Albélló et al., 1997; Rewitz et al., 2004; Hunter and Naylor, 1993; McGaw et al., 1992). Obviously,
This is a method that is heavily inclined toward researcher bias (Crothers, 1966). Previously, researchers have tried to minimize effort on this task by sampling “green” and “red” crabs over the course of one or two tidal cycles (i.e. one high and one neap tide) (Rewitz et al., 2004) or in months of the year when sampling was convenient to researchers (Rewitz et al., 2004; Albelló et al., 1997; Hunter and Naylor, 1993; Audet et al., 2008). These studies do not quantify the duration of the intermolt period in the field, and do not document the full spectrum of color change over the period of the intermolt.

More recent studies have made an effort to describe the continuous process of molting through use of a rainbow of paint swatches, but these were nonstandard department store paint swatches (Lee et al., 2005), and because the color-staging process is laborious, sample sizes were small (N<200) and sampling occasions were few (once in each location). This study made an effort to use a standard, scientifically-approved, inexpensive, published, and translatable color evaluation system to describe a very large sample of subtidal crabs (~35,000) systematically over the course of an entire year, for the purpose of describing the duration of the intermolt of green crabs in the field based on average color. Colors were described in terms of hue, chroma, and value. Knowledge of how these color measurements change and are associated over time in the system of a crustacean integument may be of use to future researchers as the biological basis of this pigmentation is further explicated. Because the molt is an important part of the green crab's reproductive cycle, this information also provided additional insight into the reproductive cycle of C. maenas in this area.

Color data indicated that females experienced their most saturated and reddest colors, indicating a population-wide imminent molt (and copulation), during June.
Females experienced their most green and washed-out colors, indicating that most of the population was done molting (and mating), by November. Future studies should confirm this reproductive window by collecting mating pairs via SCUBA survey or by another minimally-invasive unbaited method. For males, reddest colors, indicating population-wide imminent molts, were seen in spring (April) and fall (November) in both estuaries, with the majority of males having accomplished the molt by June, when females were beginning their molt. Whether these molts represent two different groups of males or two consecutive molts is unclear. In either case, male molting cycles appeared to be staggered with female molt cycles in such a way that males had hard shells when females had soft shells. This would be conducive to reproductive success, mate cradling, and larger sizes attained by males, in general. Because this effect was observed across both estuaries at the same time, day length may have played a larger role than rather than water temperature in spurring this change. This hypothesis gains credence from literature that points to photoperiod as the primary molting cue in crustaceans that molt immediately following eyestalk ablation (Aiken, 1969).

Egg-staging based on egg-color change was consistent with previously tested methods (Crothers, 1967; Audet et al., 2008; Cameron and Metaxas, 2005). Embryogenesis in the HSE appeared to take a period of months, starting approximately in January or February and being mostly accomplished by the end of June. This is consistent with studies throughout the green crab’s native and invasive range that report a four or five-month egg-carrying period (Cameron and Metaxas, 2005; Vinuesa 2007; Crothers, 1968) although a period as short as three months has been reported in Canada (Audet, 2008). The timing of egg-carrying found by these results is consistent with the temporal
findings of Berrill for coastal Maine populations, and his hypothesis that eggs are extruded in late winter in Maine instead of in late spring as they are in their native range in Britain and Holland (Berrill 1982). In the HSE, megalopae are present in their greatest numbers from July through September (Grabe, 2003), which supports Berrill’s hypothesis that megalopae settle in the summer in Northern New England rather than in the late summer and early fall as they do in their native range where mean water temperatures are warmer.

Examinations of mass-for-size relationships in order to describe distributions in male and female crabs were made in order to improve upon the efforts of previous studies. Previous studies include those made with much smaller sample sizes (Torchin et al., 2001; Crothers, 1968). The comparison of growth characteristics between these two estuaries also improves upon studies which only investigated male and female mass-for-weight relationships within one estuary (Audet et al., 2008; Torchin et al., 2001; Albelló et al., 1997). This information will allow future researchers to better understand how the sexually dimorphic rates of growth in adult green crabs can vary in two different estuarine systems within the same geographic range.

Mean size and mass attained by males and females (and by crabs in the HSE and GBE) were all statistically different, as were equations describing the relationship between CW and mass across both sexes and estuaries. Crabs in the HSE generally did not achieve as much growth as those in the GBE, and males consistently outgrew females in both estuaries. Increased time exposure to higher temperatures in the GBE may also result in larger crab size due to an increased window of metabolic activity, as green crabs are poikilotherms (Watson and Howell, 1999). Male green crabs are expected to be larger
than females, as green crabs are sexually dimorphic (Crothers, 1967) and males guard females during the mating process. In addition, the generation of a clutch of 180,000 eggs is likely a large energy expenditure for female crabs that may contribute to smaller female sizes, in general.

**Recommendations and Conclusions**

Overall, green crabs in New Hampshire were found to be more abundant in the HSE than in the GBE, and to have different operational sex ratios in the HSE and GBE. Both populations shared a reproductive window, foraging windows, and size distribution similar to those previously documented in Maine and Canadian green crabs.

Many recommendations for future restoration work in the HSE and GBE can be made based on this work. Temporally, it appears that green crab foraging activity is at a minimum in the May-September window in both the HSE and the GBE. Conveniently, this is an excellent time of the year to be conducting field work in New England, a minimally-stressful period for the release of juvenile fish, and a particularly good time for photosynthesis in brackish-water plants.

In order to minimize contact with green crabs, it is advised not to conduct extensive release or restocking work at up-estuary locations in the HSE, particularly at sites N and T-Z. Restocking and release programs in the GBE are at much lower risk for green crab damage, but work at sites F and H is least advisable. Of course, minimizing overlap with active green crab populations may not be possible, dependent on the needs of the research organism and project in question.
YOY cultured juvenile winter flounder will be at an optimal release size (>20mm) and winter flounder prey items are abundant in the GBE in the May-September window (Fairchild, 2002). In addition, careful choice of (predator-free) stocking locations for juvenile winter flounder is likely to reduce predation, as YOY fish move little when conditions (in order of likely importance: substrate, sheltering structures, and prey abundance) are good in the area of their release sites (Fairchild, 2002). At site H, flatfish burying would likely be easier than at site C due to the finer particle size of sediment there (Fairchild, 2002). In addition, winter flounder likely experience better growth rates in that area as well (Fairchild, 2002). Data from the same study that shows green crab abundance was higher but not significantly higher at our site H than it was at site C (Fairchild, 2002), but data from this study shows a significantly higher CPUE of green crabs at site H than at site C. Because natural winter flounder abundance was similar at all prospective release sites trawled in GBE (Fairchild 2002), but green crab abundance appears to be quite a bit higher at the Oyster River site, site H is not recommended as an optimal release location. In the future, green crab abundance by trapping should be estimated over the course of an entire field season at broad cove, listed as site 2 in (Fairchild, 2002), as this may be a better release area than site H, based on the sediment and prey types found at that location, as recommended by Fairchild (2002).
CHAPTER II

OPTIMIZATION OF GREEN CRAB TRAPPING EFFORTS

Introduction

Chapter one of this thesis followed the spatial and temporal distribution of green crabs in New Hampshire estuaries, with particular reference to minimizing the possible economic and ecological damage caused by these animals locally. Knowing where green crabs are is the first step to minimizing contact between green crabs and adversely-affected local projects. Previous studies have looked at ways of redesigning restocking and culturing projects so that green crab impact would be minimized by: 1) releasing fish once they were in a size class less likely to be predated (Fairchild, 2000); 2) designing cages around mussel beds and nets over clam beds that green crabs or green crabs within certain size classes could not penetrate (Davies, 1980); and 3) by attempting new methods of planting eelgrass (eg: raised lattice works) that green crabs might not bioturbate (Fred Short, unpublished data). The most effective tested methods for protecting mussels (floating rafts and protective compartments for spat) are not commercially viable (Davies, 1980), and raising cultured fish to sizes beyond crab predation represents a considerable investment in facilities, feed, and labor. An alternative method of protecting these projects from green crab predation would be to eliminate and/or reduce the presence of the crabs themselves.
Complete eradication of green crabs from the HSE and the GBE is not a reasonable goal, as New Hampshire lies well within the range of this invasive animal, (therefore allowing re-colonization from the north and south), the number of vectors for re-colonization are many, and green crab reproduction and recruitment are robust. With this in mind, it is necessary to discuss previously-tested or suggested methods of green crab removal to establish why trapping is the best method for controlling green crab populations.

**Candidate methods for green crab population control**

There are several methods used to control animal populations including biological, chemical, and physical methods. Biological population control mechanisms include stocking predators, introducing debilitating parasites, and utilization of sterilization techniques. For green crabs, biological control by increasing green crab predators is unlikely to be effective. Although the green crab has many predators in New England (ie: shorebirds, lobsters, and carnivorous fish) none of these have evolved as green crab specialists (Kuris et al., 2005).

Introduction of native parasites of *C. maenas* has been suggested as a possible biological control method for the green crab in its invasive range. Parasites that use *C. maenas* as an intermediate host (ie: nematodes) are undesirable options, as the terminal host affected is usually a vertebrate, and testing host-specificity is complicated by possible infection at several trophic levels. Nemerteans (eg: *Carcinonemertes carcinophila*) that parasitize *C. maenas* broods are a possible candidate, as some exhibit
host specificity at the subspecies level (i.e., *Carcinonemertes carcinophila imminuta* infects *Callinectes sapidus* on the east coast of the United States, but does not infect invasive green crabs within the same range) (Gibson et al., 1993). Further laboratory experiments regarding the host specificity and brood mortality impact of *Carcinonemertes carcinophila* are merited. The castrating rhizocephalan *Sacculina carcini* also has been suggested as a biological control candidate for *C. maenas* in introduced areas, but a laboratory study in which west coast conspecifics *Hemigrapsus nudus, Hemigrapsus oregonensis,* and *Pachygrapsus crassipes* were exposed to infectious *S. carcini* larvae revealed that all crab species (not just the green crab controls) were susceptible to mortality.

Introduction of transgenic individuals with inducible sterility or fatality genes is currently being probed as a solution to other nuisance invasive populations, but this research is still in its infancy (Brown and Walker, 2004; Soboleva et al., 2003; Davis et al., 1999). However, many officials are wary of releasing genetically modified individuals into the wild because of past failures, like accidental releases of genetically modified Atlantic salmon that wreaked havoc on local ecosystems (Baum, 2001).

The use of chemicals to control green crab populations has been considered and used in the past. Poison bait or direct application of carbaryl (commercial name Sevin) has been used in Oregon and Washington to control nuisance burrowing shrimp populations in Manila clam and Pacific Oyster culture (Stickney, R.R., 2009; Kern et al., 2002). Carbaryl is especially toxic to arthropods and has been suggested as a control mechanism for green crabs (Kern et al., 2002). The EPA lists carbaryl as acutely toxic to arthropods at concentrations of 0.85 μg/L and chronically toxic at concentrations of
0.5 µg/L (EPA, 2011). Toxicity margins for fish are higher, listed at 110 µg/L (acute) and 6.8 µg/L (chronic); and for vascular and nonvascular aquatic plants, the margin is 10 to 100 times higher than it is for invertebrates (EPA, 2011). The mechanism of action of this particular pesticide is damage to the nervous system by cholinesterase inhibition (EPA, 2006). Implementation of such a pesticide for the control of green crabs in New Hampshire is not recommended because this pesticide affects arthropods in general, and the state enjoys a thriving lobster fishery which likely would be adversely affected in areas of overlap with green crab habitat (revealed in chapter 1 of this thesis to be quite broad); several other species of crabs and other estuarine invertebrates would also be adversely affected (Kern et al, 2002).

Historically, the use of pesticides to control green crabs in New England has been an environmentally damaging enterprise. Experiments in Kittery, Maine in 1961 used bait poisoned with lindane, an organochlorine pesticide, to draw green crabs away from affected beds of *M. arenaria*. Catch of green crabs in affected areas declined 76% during the course of the study (Hanks, 1961), and lindane was praised as an inexpensive solution to the green crab problem. However, lindane was banned entirely for US use in 2007 by the EPA, and listed as “toxic, persistent, and bio-accumulative” (EPA, 2006). Therefore, in a historical context, use of pesticides, especially in delicate estuarine ecosystems, is heavily discouraged. Use of pesticides in New Hampshire by private companies requires state licensing and proper, updated permits (NHDA, 2005).

Biological and chemical control of green crabs in estuaries are therefore not worth implementing for diverse reasons. Physical removal of green crabs is the most favored method to control these populations.
Physical green crab removal methods include netting, trapping, and dredging. Fyke nets are an older method of trapping fish, crustaceans, and turtles, and have been used to catch green crabs by several research studies (Abello et al., 1997; Cameron and Metaxas, 2005; Rewitz et al., 2004, Mathieson and Berry, 1997). The advantage of these nets is that they can be used with minimal impact on bottom-features. These nets also can be used unbaited, although that lowers catch per unit effort (Balik et al., 2003). However, use of these nets may result in higher bycatch, particularly if they are used purposely to catch other species (ie: eels) on a seasonal basis. These nets have to be repaired more frequently than wire traps, and cannot be left to soak as long, because crabs will damage the nets and escape (Garcia-de-Lomas et al., 2010). CPUE is lower for dredging than it is for net or trap fishing, because no bait or appealing structure is used to draw crabs from a distance. However, damage to bottom features is more extensive by this method, and incidental catch of non-target species that would not be otherwise attracted by bait is higher. Impact on bottom features by wire-mesh traps is greater than it is for fyke-nets, but is less than it is for trawls. Wire mesh traps can be left in the water longer because crabs cannot destroy the mesh to free themselves, and wire-mesh traps require less maintenance and repair because they are made of more durable materials. As with fyke-nets, traps can be laid down serially.

In order to understand and develop the best method for trapping green crabs, it is necessary to discuss what catch numbers mean relative to overall green crab abundance (density). Some review of the general terminology pertinent to crab fishing and population estimation from catch numbers is therefore necessary.
Catch-per-unit-effort (CPUE) and effective-area-fished (EAF)

Catch-per-unit-effort is used to estimate the abundance of a trapped or fished animal. Units for this term are typically the number of animals captured per hour of fishing effort. In trapping, the time portion of this is the number of hours that the trap is left "soaking" in the water. CPUE is assumed to be directly correlated with the abundance of the animal in question (measured in animals per meter squared or hectare squared), although several factors can cause this assumption to be violated. Typical abundance of crabs in commercially fished areas is usually on the order of 50 to 250 crabs*ha⁻¹ (Melville-Smith, 1986). Estimates of the density of the green crab in its native range (the Atlantic coast of Europe) are as high as 20 crabs/m² on average and as high as 200 crabs/m² in optimal habitats (Carlton et al. 1995). CPUE, when regressed with environmental or animal variables, can be used to develop "catchability" equations describing the probability of catching a certain size range of animal or a certain abundance of animal for a given unit effort (Morrissy and Caputi, 1981; Miller, 1989).

The concept of effective-area fished per trap is usually defined as the distance from which a baited trap draws hungry animals. Equations estimating this figure are written as EAF = Catch/Density (Melville-Smith, 1986). This number allows for calculation of optimal trap spacing in a given area or on a long line. This number, again, can be influenced by a number of factors.
Factors that influence CPUE and EAF

CPUE and EAF may be adversely affected if: 1) animals are less likely to enter pots due to competitive interactions with conspecifics (ie: *H. americanus; C. irroratus; C. borealis*) in or around traps; 2) traps become saturated (full) before the hypothesized soak time, at which point further fishing effort does not affect CPUE; 3) animals prefer other baits or environmental food stimuli to the bait used; 4) animals are easily able to exit traps; and if 5) bait can be stolen from traps. In order to identify the best method for trapping green crabs, all of these factors that influence CPUE were investigated in a series of laboratory and field experiments.

Methods

Efficiency of bait

Efficiency of bait was calculated from chapter 1 data as grams of crab obtained for gram of bait deployed. In other words, return on bait = total weight crabs captured per trap (g)/total bait put into trap (g). Traps that were lost were not considered in this analysis.

Escapement study

To determine if green crabs could escape from the traps used in the field study (see Ch. 1), a laboratory experiment was conducted in April 2010, at the University of New Hampshire’s Coastal Marine Laboratory in New Castle, New Hampshire. A PC-222 Infra-Red (IR) sensitive video camera and two small additional IR lights were suspended at a distance of approximately 94cm and 61cm, respectively, over a 1.83m diameter tank (Fig. 1). IR-lights were used because they do not bother crabs (Elizabeth Dubofsky,
Masters candidate under Dr. Win Watson, personal communication). Video feed was relayed from this camera via a video cable to a ADVC 110 video input and into an apple macbook laptop running leopard OS. This setup was set to record one frame per second onto gawker time-lapse software. One hundred fifty crabs were held without food for 3 days in this 1.83m diameter tank that was connected to the building’s flow-through seawater system. Throughout the duration of the experiment, natural photoperiod was provided by unshaded windows. Dead crabs were removed daily to ensure cannibalism was minimal during the fasting period.

After three days of fasting, a rectangular plastic-coated wire mesh trap measuring 61X28X31cm with a single vertical chute in the top measuring 15X5X10cm deep, and baited with a single cod rack weighing approximately 454g, was dropped into the tank. The IR lights and IR video feed were started immediately. Crabs were allowed to voluntarily enter the trap. After three hours, all crabs that had not entered the trap were removed from the tank. The total number of crabs removed from the tank and that had entered the trap were recorded. The trial continued for another 25 hours simulating a typical soak time, then the final number of crabs inside and outside of the trap were counted. The video feed was then viewed to observe how animals escaped. This experiment was replicated three times in the same configuration with new crabs.
Figure 22. Video escapement tank design. An IR-sensitive camera (center, hanging) records the movement of crabs in a tank lit by two infra-red lamps (electrical-taped to the beam).

**Trap collar study**

To try to reduce crab escapement, a trap was modified and studied in the CML. A rectangular plastic-coated wire mesh trap measuring 61X28X31cm with a single vertical chute in the top measuring 15X5X10cm deep was fitted with a 10cm deep funnel inside the chute. The funnel was made of rubber matting and held together with zip-ties and hot glue.

In August 2010 at 4:00pm, 155 green crabs were placed in an unbaited unmodified (funnel-less) trap and 155 crabs in an unbaited modified (funnel-equipped) trap in a 1.83m diameter flow-through tank at CML. Natural photoperiod was provided by windows. After 24h, the number of crabs escaped from each trap was tallied. This
experiment was replicated three times using new crabs each time. After use, all crabs were frozen to death. Statistical analysis performed on these data was an independent samples t-test, equal variances not assumed ($\alpha = 0.05$), to determine if the number of crabs retained in funneled traps was significantly different from the number retained in un-funneled traps.

**Trap saturation study**

To determine the minimum time to trap saturation by green crabs, 30 baited, funneled traps (plastic-coated wire mesh trap measuring 61X28X31cm with a single vertical chute in the top measuring 15X5X10cm deep) were dropped in the Hampton River, approximately 10m apart, at 7:10 on Aug 17, 2010. Three traps were pulled every three hours for 24h, at 10:10, 13:10, 16:10, 19:10, 22:10 on 7/17 and 1:10, 4:10, and 7:10 on 7/18. An additional three traps were pulled at 19:10 on 7/18 and 7:10 on 7/19. The number of crabs in each trap was tallied. After each haul, all crabs were removed from the estuary.

Mean catch numbers were graphed over time and a curvilinear regression was performed on the data. The derivative of this regression equation was taken to determine the time at which the slope ceased increasing. This number was taken to be saturation time.

**Laboratory bait preference study**

Bait preferences of green crabs in a laboratory setting were assessed in August 2010. Green crabs were placed in individual plastic containers floating in a flow-through tank at Jackson Estuarine Laboratory in Durham, New Hampshire and food was withheld
for three days. A plexiglass Y-maze approximately 1.85m in length was constructed outside, such that the grade ran slightly downhill from the two-sided end of the maze to the one-sided end (Fig. 2). The water in the maze was approximately 9cm deep throughout, and inflow on the two-sided end was maintained at 65-70ml/sec, consistent on both sides of the maze. The maze was concealed by a black tarp, so that shadows from the sun would not affect crab behavior. Ambient water temperature varied from 20 to 25°C. Sample baits used were previously frozen, 10g pieces of defrosted salmon, cod, herring, and haddock. Bait buoyancy was counterweighted with stainless-steel screws. A fresh bait sample was used at the beginning of each trial, and the Y-maze was drained by siphoning, and rinsed thoroughly between trials. Careful consideration was made such that trials within a certain combination of baits were evenly distributed between the right and left sides of the maze; the position of each bait type was switched from left to right and vice versa between trials. During each trial, a single crab (CW between 47 and 60mm) was introduced into the Y-maze in a plastic mesh container that was held at the starting line for a one-minute acclimation period. The container was then lifted off of the crab and the crab was allowed to walk toward the preferred bait. Preference was considered when the crab walked directly toward one of the two baits and began feeding on the sample. Crabs that displayed erratic or non-feeding behavior (walking behind the starting line and hunkering in a corner, or failing to move after five minutes) were discarded.

All (4 choosing 2 = 6) possible bait combinations were tested, with twenty trials per combination (Fig. 24). Twenty control trials were conducted with the same bait (cod) at both ends of the maze in an effort to assess right-left tendency (Fig. 24).
Figure 23. A photo of the experimental Y-maze utilized in the laboratory bait preference experiment. This maze was covered with a black tarp to eliminate sunlight (which is removed in this picture for clear visual). Flow travelled from the bottom left hand corner to the top right hand corner of this photo. An outlet drain was located behind the spill-bar shown at the far end of the photo. The maze was tube-siphoned, rinsed, re-siphoned, and refilled between trials.
Pearson's chi-square tests were used to test the hypotheses that 1) A bait was preferred over any other bait (N=120 overall and N=20 for each sample); 2) That a “favorite” or “least favorite” bait existed over all other choices (N=60 for each sample) by comparing the frequency of the choice of any given bait to the choice of all other baits provided; and 3) That crabs had left of right handed leanings (N=20 for purpose controls and N=120 overall).

**Field bait preference study**

On October 21 2010, at 14:30, 15 traps were baited (5 bait treatments x 3 replicates) and deployed approximately 9m apart in 3.4m of water in the Hampton River to test green crab bait preference *in situ*. Bait treatments consisted of 454g chunks of cod, haddock, salmon, salted herring, or no bait (control). The water temperature was 12°C,
water salinity was 31ppt, and the tide was falling (low tide was at 17:26). All of these traps were pulled after a three hour soak period and the total number of crabs was counted. A one-way between-S ANOVA followed by a Tukey’s HSD post-test was conducted to compare the mean number of *C. maenas* captured by each of the four different baited traps, and the number of *C. maenas* obtained from unbaited control traps. Significant differences were interpreted as preferences.

**Effect of competitors on average catch per trap**

The effect of competitors on average catch per trap was assessed from Chapter 1 data. Possible competitor species considered were *H. americanus, C. borealis,* and *C. irroratus.* Trap catches in individual traps without competitor species, and in all observed combinations of competitors, were calculated for both estuaries. These data were averaged and analyzed for significant differences by one-way Kruskal-Wallis ANOVA (*α*=0.05) followed by Dunn’s nonparametric significance test of stepwise comparisons.

**Results**

**Efficiency of bait**

Return on bait in the GBE was 1.98 g crabs/g bait deployed. Return on bait in the HSE was 19.72 g crabs/g bait deployed.
**Escapement study**

Table 8: Number of crabs that escaped from unmodified traps during video observation.

<table>
<thead>
<tr>
<th>Trial</th>
<th>After 3 hours</th>
<th>After 25 hours</th>
</tr>
</thead>
<tbody>
<tr>
<td></td>
<td>Number Crabs removed</td>
<td>Number Crabs inside</td>
</tr>
<tr>
<td>Trial 1</td>
<td>111</td>
<td>39</td>
</tr>
<tr>
<td>Trial 2</td>
<td>131</td>
<td>19</td>
</tr>
<tr>
<td>Trial 3</td>
<td>125</td>
<td>25</td>
</tr>
</tbody>
</table>

During trial 1, 2 out of 111 crabs (5.1%) escaped (Table 1). There were no other escapees in the other 2 trials. Although the exact method of escape was not clear from this video, crabs have been observed escaping from these traps by a combination of climbing and weak swimming movements (Fulton, personal observation).
Figure 25: A screenshot of time-lapse video of trial 2 in which bait stealing through the side of the trap is visible (indicated by the red arrow).

In this figure, a technique by which crabs grabbed the bait and pulled it toward the side of the trap so it could be eaten through the mesh without entering the trap is shown. To some extent, this behavior undermined the function of a trap entrance in these traps.

Figure 26: Screenshots of time-lapse video of trial one in which a nighttime escape is visible.
The crab has just climbed out of the trap (post-escape; left panel) and walks away, down the side of the trap, to safety (right panel). It was followed by another crab within the same five minute period. The method used to reach the funnel from the inside of the trap was unclear because of light reflection.

**Trap collar study**

Table 9. Escapement from funneled and unfunneled traps.

<table>
<thead>
<tr>
<th>Trial</th>
<th>Remain in funneled</th>
<th>Escaped funneled</th>
<th>Percent escaped funneled</th>
<th>Remain in unfunneled</th>
<th>Escaped unfunneled</th>
<th>Percent escaped unfunneled</th>
</tr>
</thead>
<tbody>
<tr>
<td>1</td>
<td>150</td>
<td>5</td>
<td>3.23</td>
<td>133</td>
<td>22</td>
<td>14.19</td>
</tr>
<tr>
<td>2</td>
<td>149</td>
<td>6</td>
<td>3.87</td>
<td>140</td>
<td>15</td>
<td>9.68</td>
</tr>
<tr>
<td>3</td>
<td>155</td>
<td>0</td>
<td>0.00</td>
<td>146</td>
<td>9</td>
<td>5.81</td>
</tr>
</tbody>
</table>

Statistical analysis revealed that the two groups of traps (collared and uncollared) did not retain significantly different numbers of crabs, but the p-value for this figure bordered on statistical significance (p=0.07).
Trap saturation study

Table 10. Raw data for trap saturation study include soak time and mean catch for each haul (average of 3 traps).

<table>
<thead>
<tr>
<th>Date</th>
<th>Trap Pull Time</th>
<th>Soak Time (h)</th>
<th>Total crabs T1</th>
<th>Total crabs T2</th>
<th>Total crabs T3</th>
<th>Average</th>
<th>SEM</th>
</tr>
</thead>
<tbody>
<tr>
<td>17-Aug</td>
<td>10:10</td>
<td>3.00</td>
<td>9</td>
<td>6</td>
<td>54</td>
<td>23.00</td>
<td>15.52</td>
</tr>
<tr>
<td>17-Aug</td>
<td>13:10</td>
<td>6.00</td>
<td>28</td>
<td>78</td>
<td>71</td>
<td>59.00</td>
<td>15.63</td>
</tr>
<tr>
<td>17-Aug</td>
<td>16:10</td>
<td>9.00</td>
<td>51</td>
<td>97</td>
<td>38</td>
<td>62.00</td>
<td>17.90</td>
</tr>
<tr>
<td>17-Aug</td>
<td>19:10</td>
<td>12.00</td>
<td>55</td>
<td>87</td>
<td>168</td>
<td>103.33</td>
<td>33.63</td>
</tr>
<tr>
<td>17-Aug</td>
<td>22:10</td>
<td>15.00</td>
<td>59</td>
<td>63</td>
<td>71</td>
<td>64.33</td>
<td>3.53</td>
</tr>
<tr>
<td>18-Aug</td>
<td>1:10</td>
<td>18.00</td>
<td>74</td>
<td>89</td>
<td>35</td>
<td>66.00</td>
<td>16.09</td>
</tr>
<tr>
<td>18-Aug</td>
<td>4:10</td>
<td>21.00</td>
<td>23</td>
<td>71</td>
<td>94</td>
<td>62.67</td>
<td>20.92</td>
</tr>
<tr>
<td>18-Aug</td>
<td>7:10</td>
<td>24.00</td>
<td>61</td>
<td>200</td>
<td>114</td>
<td>125.00</td>
<td>40.50</td>
</tr>
<tr>
<td>18-Aug</td>
<td>19:10</td>
<td>36.00</td>
<td>58</td>
<td>88</td>
<td>83</td>
<td>76.33</td>
<td>9.28</td>
</tr>
<tr>
<td>19-Aug</td>
<td>11:10</td>
<td>48.00</td>
<td>110</td>
<td>105</td>
<td>128</td>
<td>114.33</td>
<td>6.98</td>
</tr>
</tbody>
</table>

Over time, catch in experimental traps appeared to reach a maximum, although there was quite a bit of variability in catch, resulting in a $R^2$ value of 0.52.

Figure 27. Average number of crabs captured in standard traps with increasing soak time.
The best fit equation for catch over time, \( y = 26.268 \ln(x) + 5.0757 \), has a derivative \( \frac{df}{dx} = \frac{26.268}{x} \). As \( \frac{df}{dx} \) approaches zero, \( x \) approaches 26.268 hours, and additional fishing effort yields negligible additional catch.

**Laboratory bait preference study**

In pairwise trials, green crabs preferred salmon over cod (\( p=0.03 \)) and salted herring over cod (\( p=0.03 \)). Green crabs chose salted herring as their favorite over all other baits more frequently than was expected (\( p=0.04 \)), and cod as their least favorite bait, \( p=0.01 \). Crabs did not show a clear left or right tendency in the 20 control trials (\( p=1 \)) or overall (\( p=0.09 \)).
Figure 28. Results of chi-squared tests for bait preference

Q1) Do pairwise preferences exist?

- Cod (10) v Haddock (10): \( \chi^2 = 0, p = 1.00, \text{NO} \)
- Cod (5) v Herring (15): \( \chi^2 = 5, p = 0.03, \text{YES, Herring} \)
- Cod (5) v Salmon (15): \( \chi^2 = 5, p = 0.03, \text{YES, Salmon} \)
- Haddock (9) v Salmon (11): \( \chi^2 = 0.20, p = 0.65, \text{NO} \)
- Haddock (7) v Herring (13): \( \chi^2 = 1.80, p = 0.18, \text{NO} \)
- Herring (11) v Salmon (9): \( \chi^2 = 0.20, p = 0.65, \text{NO} \)

Q2) Is there a “favorite” or “least favorite” bait?

- Cod (20) v All other baits (40): \( \chi^2 = 6.60, p = 0.01, \text{YES, Cod is least favorite} \)
- Haddock (26) v All other baits (34): \( \chi^2 = 1.07, p = 0.30, \text{NO} \)
- Herring (39) v All other baits (21): \( \chi^2 = 4.33, p = 0.04, \text{YES, Herring is favorite} \)
- Salmon (35) v All other baits (25): \( \chi^2 = 1.67, p = 0.20, \text{NO} \)

Q3) Is there a clear right or left tendency?

- Cod (L) (10) v Cod (R) (10): \( \chi^2 = 0, p = 1.0, \text{NO} \)
- All baits (left side) (60) v All baits (right side) (80): \( \chi^2 = 2.86, p = 0.09, \text{NO} \)

Results of chi-squared tests for bait preference revealed that crabs preferred herring over cod and salmon over cod, but no other preferences existed in pairwise trials. In comparisons of each bait to all other baits against which it was compared, cod was found to be the least favorite of all baits, and herring was found to be the most favorite.
**Field bait preference study**

Table 11. Number of crabs attracted to different bait options in the field

<table>
<thead>
<tr>
<th>Bait</th>
<th>Number Crabs</th>
<th>Average</th>
<th>$\theta$</th>
</tr>
</thead>
<tbody>
<tr>
<td>Control 1</td>
<td>1</td>
<td>1.33</td>
<td>0.57</td>
</tr>
<tr>
<td>Control 2</td>
<td>1</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Control 3</td>
<td>2</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salmon 1</td>
<td>88</td>
<td>149.67</td>
<td>75.59</td>
</tr>
<tr>
<td>Salmon 2</td>
<td>234</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Salmon 3</td>
<td>127</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haddock 1</td>
<td>234</td>
<td>218.67</td>
<td>26.59</td>
</tr>
<tr>
<td>Haddock 2</td>
<td>234</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Haddock 3</td>
<td>188</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cod 1</td>
<td>323</td>
<td>283.00</td>
<td>68.42</td>
</tr>
<tr>
<td>Cod 2</td>
<td>322</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Cod 3</td>
<td>204</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herring 1</td>
<td>36</td>
<td>42.67</td>
<td>14.22</td>
</tr>
<tr>
<td>Herring 2</td>
<td>59</td>
<td></td>
<td></td>
</tr>
<tr>
<td>Herring 3</td>
<td>33</td>
<td></td>
<td></td>
</tr>
</tbody>
</table>
Figure 29. Average number of crabs attracted to different bait options in the field (replicate N=3). Error bars are ±1SD. Homogeneous subsets (α=0.05) are denoted by lowercase letters.

In the field, the number of crabs attracted by unbaited traps was lowest, followed by traps baited with herring, salmon, haddock, and cod, which attracted the most crabs per trap.

**Effect of competitors on average catch per trap**

It was found that traps that contained *C. borealis* and/or *H. americanus* caught fewer green crabs than traps that did not contain one of these competitors. Traps with *C. irroratus* did not always catch fewer green crabs than traps that contained only green crabs (Figure 29).
Figure 29. Effect of potential competitors on average catch per trap in HSE and GBE. Error bars are ±1 SEM. Lowercase letters indicate significant differences (α=0.05).

**GBE**

**HSE**

Competitor Key

1 = *C. borealis*

2 = *C. irroratus*

3 = *H. americanus*

4 = *C. irroratus* + *C. borealis*

5 = *C. irroratus* + *H. americanus*

6 = *C. borealis* + *H. americanus*

7 = No competitor
Discussion

Bait used on crabbing in GBE yielded twice its mass in crabs. This makes fishing green crabs in GBE seem uneconomical, once effort expended, labor fees, bait cost, gear costs, dock expenses, and gas spent are factored into the equation.

Table 12. Profitability of hypothetical green crabbing operation in GBE (based on expenditures encountered during this study)

<table>
<thead>
<tr>
<th>Item</th>
<th>Expense ($)</th>
<th>Profit ($)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bait (18kg at $2.2/kg)</td>
<td>40</td>
<td>0</td>
</tr>
<tr>
<td>Gas (10gallons)</td>
<td>40</td>
<td>0</td>
</tr>
<tr>
<td>Labor (2 persons*3 hours)</td>
<td>90</td>
<td>0</td>
</tr>
<tr>
<td>Wear and tear (on 40 traps)</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>Green crabs (36kg at $1.1/kg)</td>
<td>0</td>
<td>39.6</td>
</tr>
<tr>
<td>Operating income</td>
<td>-150.4</td>
<td></td>
</tr>
</tbody>
</table>

However, return on bait in HSE was ten times higher: 19.72 g crabs/g bait deployed. This figure is highly dependent on many factors (season, salinity, temperature), as was discussed in Chapter 1. In seasons of peak yield, a boat fishing in HSE with these (or similar existing) traps could expect the following economics:

Table 13. Profitability of hypothetical green crabbing operation in HSE (based on expenditures encountered during this study)

<table>
<thead>
<tr>
<th>Item</th>
<th>Expense ($)</th>
<th>Profit ($)</th>
</tr>
</thead>
<tbody>
<tr>
<td>Bait (18kg at $2.2/kg)</td>
<td>40</td>
<td>0</td>
</tr>
<tr>
<td>Gas (10gallons)</td>
<td>40</td>
<td>0</td>
</tr>
<tr>
<td>Labor (2 persons*3 hours)</td>
<td>90</td>
<td>0</td>
</tr>
<tr>
<td>Wear and tear (on 40 traps)</td>
<td>20</td>
<td>0</td>
</tr>
<tr>
<td>Green crabs (364kg at $1.1/kg)</td>
<td>0</td>
<td>400.4</td>
</tr>
<tr>
<td>Operating income</td>
<td>210.4</td>
<td></td>
</tr>
</tbody>
</table>

However, yield might have been higher if several aspects of trap design had been
improved upon. As was seen in video escapement studies, crabs were able to drag bait to the side of the trap and consume it through the mesh. If the bait had been hung on a hook in a bag (as it is in lobster traps), or in an inaccessible well (as in commercial crab traps), more animals would have been forced to enter the trap to feed. In addition, commercial crab pots used for blue crabs and rock crabs are closer to the size of lobster pots—considerably larger than the traps used in this study (Sturdivant and Clark, 2010). Those traps would probably saturate more slowly (Figure 5) if implemented for this purpose.

The applications of the saturation time obtained in the saturation study are limited by the fact that the study was conducted during a month when green crab catches were at a seasonal low (Chapter 1). To increase the applicability of this study, it should be conducted again during a high-catch month and in an area where crab density is generally greater to ensure that saturation in those contexts does not happen more quickly. However, until further experiments are conducted, the trap soak period tested in chapter 1 of this thesis appears adequate.

All video-observed escapements happened at night, which supports the hypothesis that crabs are more active at night. Escapement occurred only in experiments in which larger numbers of crabs entered the traps (>39 crabs), and was probably facilitated by crabs climbing on top of each other. Crabs probably escaped the funnel using a combination of climbing and weak swimming (personal observation), and were most likely aided by the lightly rippled texture of the rubber used in this experiment. As was seen in the funneled-unfunneled experiments, funnels made of the materials tested in this study did not significantly reduce escapement, though the margin for significance was close. In the future, an experiment with a greater number of trials should be
conducted, and chutes made of a slippery plastic fabric would probably make escapement more difficult.

In laboratory maze experiments, green crabs chose salted herring over all other bait choices more frequently than was expected, and chose all other baits over cod more frequently than was expected. Preference of salmon over herring in pairwise trials is probably an anomaly that would be eliminated by conducting a larger number of trials, as salmon did not come close to achieving favoritism over all other baits overall. Field bait preference indicated that green crabs preferred haddock and cod over salmon and salted herring. This contradictory finding suggests a few possibilities: 1) laboratory results may have been influenced by an experimental artifact. A maze with a plug-bottom drain would have been better for conducting this experiment, as the maze used in this case had to be siphoned and rinsed between trials, leaving the possibility that cleaning was not perfect and odor stimuli may have remained between trials. 2) Alternatively, soak period in the field experiment was three hours, compared to about six minutes for a maze trial. It could be that crustacean chemoattractants (mostly consisting of low-molecular-weight stimluants like quaternary ammonium compounds, nucleotides, nucleosides, and amino acids) in the bait plumes of the oily fish samples mostly disperse in the period between five minutes and three hours, while non-oily fish samples disperse these chemoattractants more evenly over a longer period of time (Carr et al, 1996). Further experiments should be conducted to investigate whether (and if so, how) soak time influences bait attractiveness.

Previous studies have found that crabs prefer fresh bait (Sturdivant and Clark, 2010), and all of the baits used in the field and lab study were previously frozen, which
was suboptimal. However, local fishermen in HSE state that haddock and cod are optimal baits for green crabs (personal communication), and the field data gathered in this experiment reinforces this notion. The catch numbers observed in this field study may be an artifact of the layout of experimental traps or the nutritional needs of the crabs foraging during the experimental season, therefore, replication of these results should be attempted in several different locations and seasons.

The finding that, on average, fewer green crabs were found in traps containing at least one *H. americanus* or *C. borealis* can be attributed to several possibilities. It is known that *H. americanus* defend and maintain territories, and that they have been known to defend food resources within baited traps, fending off other conspecifics (Sturdivant and Clark, 2010). In a laboratory experiment simulating field densities of subadult and adult *C. maenas*, and adult *H. americanus* and *C. borealis*, adult *C. maenas* suffered mortality by both conspecifics, but considerably higher mortality to *H. americanus*, which consumed 27% of stocked *C. maenas* within 24h (*C. borealis* consumed 5%). In the presence of *H. americanus*, *C. maenas* displayed significantly reduced patterns of nighttime behavior, including more hiding and climbing/clambering behaviors, presumably in order to avoid interactions with lobsters (League-Pike and Shulman, 2009). Although *C. borealis* possess broader chelae and exceed *C. maenas* in size, they are not particularly efficient predators of green crabs because they are not as agile (League-Pike and Shulman, 2009). However, in an enclosed space (e.g. a crab trap), a green crab’s advantage may be diminished.

It is generally assumed that *C. irroratus* do not present a significant threat to *C. maenas*, because they are similar in size (slightly larger) and have only modestly larger
chelae (League-Pike and Shulman, 2009; Moody and Steneck, 1993). Laboratory experiments examining the effect of the presence of same-sized *C. maenas* on the growth and physical condition of juvenile *C. irroratus* found that the presence of *C. maenas* in rearing conditions results in slightly retarded growth of *C. irroratus* juveniles (longer intermolt, smaller molt increments, and higher hepatopancreas lipid reserves) relative to *C. irroratus* juveniles raised with other *C. irroratus* of the same size, (due to competition for food resources). However, once *C. irroratus* juveniles reach 19-22mm, this growth retardation is quickly reversed (Breen and Metaxas, 2009) as *C. maenas* sharing the same territory finally represent an additional food subsidy (Breen and Metaxas, 2009). The results of this study indicate that it is doubtful that *C. irroratus* represent a deterrent to green crabs entering traps; in fact, in some cases traps containing *C. irroratus* had higher green crab catches than traps that did not. It is unclear whether this means that one of these two species attracts the other, that the two species undergo aggressive interactions that don’t affect trap entrance (as seen in Sturdivant and Clark, 2010), or that the two species simply coexist. Trap-mounted camera studies in traps seeded with all of these conspecifics would shed light on the interactions that cause this effect, while allowing researchers to control trials and environmental variables.

**Conclusion**

Although the traps used in this study were not ideal, their shortcomings, as revealed by these experiments, can easily be remedied in future design efforts. Slippery fabric funnels (to minimize escapement), larger trap size (to accommodate larger catches and decrease escapement), cod or haddock as bait, and use of bait hooks or wells (to minimize bait stealing) would all likely increase catch. For ease, traps could be laid
serially on lines. As mentioned in Chapter 1, the spring and fall seasons are particularly productive in the HSE for green crab catches. In New Hampshire, there is no season on black sea bass or striper, so as long as fishermen are careful not to glut the market with green crabs, a seasonal bait fishery is a possibility for export to New York and New Jersey. The considerable return of crab biomass in the HSE constitutes a valuable resource whose other possible applications will be discussed in chapter three of this thesis.
III. NUTRITIONAL PROFILE OF THE GREEN CRAB

Introduction

Chapters 1 and 2 of this thesis established that the HSE contains a large and easily-harvested biomass of green crabs, and that trapping was the most plausible method for controlling this population. Experimental trap catch in the HSE averaged 386 crabs per trap (1 SEM=±1.8), and the return on bait was approximately 20:1 (green crab wgt. to bait wgt.). Over the course of the yearlong study, 0.89mt of green crabs were removed from the HSE. As effective area fished for the traps used in this study has not yet been investigated, it is impossible to correlate catch numbers directly with density of green crabs. Even after implementation of such a study, CPUE variations as a result of abiotic factors like water temperature and day length would have to be taken into consideration (Seed and Murray, 2010). However, it is highly likely that catch numbers could be increased by making minor modifications to the traps used in this study, and by fishing during seasons of greatest foraging activity.

Large-scale green crab removal from the HSE could be established on the basis of a bounty program or as an emerging market. Bounty programs, in which fishermen are paid from a subsidy to remove pest species, have been previously tested for the removal of green crabs in areas like Martha's Vineyard (Walton, 2000). Research shows that, in
areas other than small embayments, these programs do not appear to decrease the within-year or among-year numbers of *C. maenas* in the area fished (Walton, 2000). Further, the reward established for removal of a pest species in such a program must be set high enough to be worth the fishing effort. However, if the reward is too valuable, culturing of the species, additional introduction of the species into the area of concern, or fishing outside the concerned area may become an issue (Kern, 2002). Development of a sustainable fishery (market) for *C. maenas* is therefore more appealing than the introduction of a bounty program.

Most of the established fisheries for *C. maenas* are located within the animal's native range in Europe. A European fishery for green crabs as angling bait (removal of ~1,000,000 crabs/year) exists in Britain (Sheehan et al., 2008), where crabs are 'tiled'. In the process of tiling, shingles are driven into mudflats, providing artificial shelter for molting crabs (~10% of catch), which are then harvested (berried females are forbidden). However, research suggests that the refugia provided by this method may, in fact, contribute to green crab population increases (Sheehan et al., 2008) and to a decrease in variety and quantity of species of macro-infauna in the area tiled, mostly due to trampling associated with tile access (Sheehan et al., 2010).

A fishery for *C. maenas* as a delicacy for humans and as a scent for seafood-based products (Pascoal et al., 2009) occurs in Portugal, where the majority of captured crabs are exported live to Spain. In 1997, the productivity of this fishery (together with a similar fishery in France) was estimated at 900 mt/year (Klassen and Locke, 2007). About half of Portuguese-exported green crabs are consumed in Spain and the rest are re-exported from Spain (Gomes, 1988). This fishery is a good model market to study.
because evidence suggests that high catch years actually have contributed to decreases in crab CPUE (evidence of overfishing) (Gomes 1988, 1991).

Because green crabs are relatively small-bodied, shelling by hand is too labor intensive for a green crab meat product to be profitable (Skonberg and Perkins, 2002). Therefore, any potential commercial use for this organism would have to use whole crabs. Recent studies have explored use of whole green crabs (macerated) in Portuguese-inspired food products like empanadas. These have been met with favorable consumer reviews (Galetti, 2010). However, these are niche markets in North America. Other markets (e.g. chum replacement for fishmeal substitutes) should be considered as outlets for this raw material.

The nutritional composition of a representative sample (as caught in the field) of whole green crabs has not yet been published, and this is a crucial first step for the development of uses. Both proximate and fatty-acid/amoio-acid composition analyses provide information needed to formulate, test, and cost-analyze potential aquaculture (feed additive or partial fish meal replacement) markets for this pest species. Ash content and composition can be a limiting factor in some aquaculture applications because of intestinal and visual ailments associated with high ash contents in freshwater fish diets (Donahue et al, 1998; Richardson et al, 1985). For these reasons, calcium, zinc, and potassium content of the crabs need to be measured. Because *C. maenas* bioaccumulates mercury (Elumalai et al, 2007), mercury content also should be analyzed.

Previously published nutritional analyses of green crabs include proximate analysis, fatty acid profile, and amino acid profile of claw and leg meat separately (Skonberg and Perkins, 2002), and of leg meat homogenate (Naczk et al., 2004). Chitin,
total carotenoids, total fatty acid and total nitrogen content of *C. maenas* shell (Naczk et al., 2004), and fatty acid profile of *C. maenas* hepatopancreas (Andersen et al., 2000) also have been reported. However, none of these studies used a representative random sample of the range of crabs (size, sex, molt stage, etc.) that would be caught in a commercial crab trap, and none of them considered the nutritional profile of the whole animal. This current analysis provides missing information regarding the nutritional composition of whole green crabs. The nutritional profile of whole green crab homogenate was analyzed in order to determine if green crabs would be appropriate for the (partial) replacement of fish meal in agriculture/aquaculture applications. Other uses for crab homogenate also were considered.

**Methods**

Green crabs were collected in NH waters in March 2010 in rectangular plastic-coated wire mesh traps measuring 61X28X31cm with a single vertical chute in the top measuring 15X5X10cm deep, and baited with a single cod rack each weighing approximately 454g. Three random 1.86 kg samples of whole crabs were selected from these traps, snap-frozen on dry ice, and sent to New Jersey Feed Labs (Ewing, NJ) for nutritional analyses. There, the samples first were macerated in a meat grinder and 14 g of each sample then was homogenized for testing. Proximate analysis of these samples was accomplished according to Association of Analytical Chemists (AOAC) methods 990.03, 930.15, 920.39, 978.10, and 942.05. Calcium, phosphorus, and zinc concentrations were assessed via AOAC methods 985.01 and 984.27. Mercury content was assessed via AOAC method 975.08, amino acid profiles were assessed via AOAC methods 994.12, 985.28, 988.15, and 994.12, and fatty acid profiles were determined via
AOAC method 963.22 (AOAC, 2011). All nutritional parameters for whole green crab meal were compared to those of whole ground Pacific menhaden, *Brevoortia patronus*, which comprises approximately 90% of forage fish material for US fishmeal production, annually, by weight (IFFO, 2011; IFFO, 2009).

**Results**

The triplicate samples are reported as individual scores (GC1, GC2, GC3), averages (GC Avg), and averages ±1SD (GC ±0) in the following tables.

Table 14. Proximate composition (sample %) of whole green crab meal. Statistics (sample %) from whole ground menhaden (*Brevoortia patronus*) are shown for comparison (menhaden values are from Lanier et al (1983), Dubrow et al., 1976, and Hale et al., 1991).

<table>
<thead>
<tr>
<th>Sample Content (%)</th>
<th>GC1</th>
<th>GC2</th>
<th>GC3</th>
<th>Menhaden</th>
<th>GC Avg</th>
<th>GC ±0</th>
</tr>
</thead>
<tbody>
<tr>
<td>Moisture</td>
<td>68.12</td>
<td>67.44</td>
<td>68.32</td>
<td>68</td>
<td>67.22</td>
<td>66.76-67.68</td>
</tr>
<tr>
<td>Protein</td>
<td>12.3</td>
<td>12.5</td>
<td>12</td>
<td>15</td>
<td>12.27</td>
<td>12.02-12.52</td>
</tr>
<tr>
<td>Fat</td>
<td>0.16</td>
<td>0.29</td>
<td>0.17</td>
<td>14</td>
<td>0.21</td>
<td>0.13-0.28</td>
</tr>
<tr>
<td>Fiber</td>
<td>3.03</td>
<td>2.82</td>
<td>2.75</td>
<td>2</td>
<td>2.65</td>
<td>2.2-3.10</td>
</tr>
</tbody>
</table>
Table 15. Fatty acid composition (% relative basis) of whole green crab homogenate. Fatty acid values for oil of whole ground menhaden (*Brevoortia patronus*) (also % relative basis) are 1982 year totals from Joseph (1985).

<table>
<thead>
<tr>
<th>Fatty Acid</th>
<th>Sample 1</th>
<th>Sample 2</th>
<th>Sample 3</th>
<th>Menhaden</th>
<th>GC Average</th>
<th>GC ±0</th>
</tr>
</thead>
<tbody>
<tr>
<td>12:0</td>
<td>0.32</td>
<td>0.32</td>
<td>0.19</td>
<td>N/A</td>
<td>0.28</td>
<td>0.20-0.35</td>
</tr>
<tr>
<td>14:0</td>
<td>1.82</td>
<td>2.02</td>
<td>1.85</td>
<td>9.20</td>
<td>1.90</td>
<td>1.79-2.00</td>
</tr>
<tr>
<td>14:1</td>
<td>0.22</td>
<td>0.28</td>
<td>0.23</td>
<td>0.20</td>
<td>0.24</td>
<td>0.21-0.28</td>
</tr>
<tr>
<td>15:0</td>
<td>1.05</td>
<td>1.03</td>
<td>1.04</td>
<td>0.60</td>
<td>1.04</td>
<td>1.03-1.05</td>
</tr>
<tr>
<td>16:0</td>
<td>16.39</td>
<td>14.96</td>
<td>15.34</td>
<td>19.80</td>
<td>15.56</td>
<td>14.82-16.30</td>
</tr>
<tr>
<td>16:1</td>
<td>8.39</td>
<td>7.90</td>
<td>7.88</td>
<td>11.90</td>
<td>8.06</td>
<td>7.77-8.35</td>
</tr>
<tr>
<td>16:2</td>
<td>0.22</td>
<td>0.25</td>
<td>0.30</td>
<td>1.70</td>
<td>0.26</td>
<td>0.22-0.30</td>
</tr>
<tr>
<td>17:0</td>
<td>0.93</td>
<td>0.93</td>
<td>0.85</td>
<td>0.80</td>
<td>0.90</td>
<td>0.86-0.95</td>
</tr>
<tr>
<td>17:1</td>
<td>0.85</td>
<td>1.11</td>
<td>0.89</td>
<td>N/A</td>
<td>0.95</td>
<td>0.81-1.09</td>
</tr>
<tr>
<td>18:0</td>
<td>3.85</td>
<td>3.57</td>
<td>3.26</td>
<td>N/A</td>
<td>3.56</td>
<td>3.26-3.86</td>
</tr>
<tr>
<td>18:1Δ9</td>
<td>16.75</td>
<td>14.32</td>
<td>14.34</td>
<td>8.2</td>
<td>15.14</td>
<td>13.74-16.53</td>
</tr>
<tr>
<td>18:1Δ7</td>
<td>5.05</td>
<td>4.59</td>
<td>5.01</td>
<td>3.00</td>
<td>4.88</td>
<td>4.63-5.14</td>
</tr>
<tr>
<td>18:2Δ6</td>
<td>3.92</td>
<td>3.02</td>
<td>2.25</td>
<td>1.1</td>
<td>3.06</td>
<td>2.23-3.90</td>
</tr>
<tr>
<td>18:3Δ6</td>
<td>0.12</td>
<td>0.23</td>
<td>0.22</td>
<td>0.6</td>
<td>0.19</td>
<td>0.13-0.25</td>
</tr>
<tr>
<td>18:3Δ3</td>
<td>0.76</td>
<td>0.76</td>
<td>0.84</td>
<td>0.8</td>
<td>0.79</td>
<td>0.74-0.83</td>
</tr>
<tr>
<td>18:4Δ3</td>
<td>0.00</td>
<td>0.44</td>
<td>0.40</td>
<td>2.1</td>
<td>0.28</td>
<td>0.04-0.52</td>
</tr>
<tr>
<td>20:0</td>
<td>0.00</td>
<td>0.16</td>
<td>0.00</td>
<td>N/A</td>
<td>0.05</td>
<td>0-0.15</td>
</tr>
<tr>
<td>20:1Δ11</td>
<td>2.09</td>
<td>1.93</td>
<td>2.22</td>
<td>N/A</td>
<td>2.08</td>
<td>1.93-2.22</td>
</tr>
<tr>
<td>20:1Δ9</td>
<td>3.65</td>
<td>3.91</td>
<td>3.40</td>
<td>1.2</td>
<td>3.65</td>
<td>3.40-3.90</td>
</tr>
<tr>
<td>20:1Δ7</td>
<td>2.16</td>
<td>2.06</td>
<td>2.47</td>
<td>N/A</td>
<td>2.23</td>
<td>2.01-2.44</td>
</tr>
<tr>
<td>20:2Δ6</td>
<td>1.54</td>
<td>1.51</td>
<td>1.66</td>
<td>N/A</td>
<td>1.57</td>
<td>1.49-1.65</td>
</tr>
<tr>
<td>20:3Δ3</td>
<td>0.00</td>
<td>0.13</td>
<td>0.41</td>
<td>N/A</td>
<td>0.18</td>
<td>0-0.39</td>
</tr>
<tr>
<td>20:4Δ6</td>
<td>2.38</td>
<td>2.60</td>
<td>2.75</td>
<td>1.00</td>
<td>2.58</td>
<td>2.39-2.76</td>
</tr>
<tr>
<td>20:5Δ3</td>
<td>8.19</td>
<td>8.69</td>
<td>9.32</td>
<td>13.50</td>
<td>8.73</td>
<td>8.17-9.30</td>
</tr>
<tr>
<td>22:1Δ11</td>
<td>2.87</td>
<td>3.43</td>
<td>2.66</td>
<td>N/A</td>
<td>2.99</td>
<td>2.59-3.38</td>
</tr>
<tr>
<td>22:1Δ9</td>
<td>0.00</td>
<td>0.41</td>
<td>0.42</td>
<td>N/A</td>
<td>0.28</td>
<td>0.04-0.52</td>
</tr>
<tr>
<td>22:4Δ6</td>
<td>0.44</td>
<td>0.54</td>
<td>0.54</td>
<td>N/A</td>
<td>0.51</td>
<td>0.45-0.56</td>
</tr>
<tr>
<td>22:5Δ3</td>
<td>1.19</td>
<td>1.21</td>
<td>1.44</td>
<td>2.30</td>
<td>1.28</td>
<td>1.14-1.42</td>
</tr>
<tr>
<td>22:6Δ3</td>
<td>7.24</td>
<td>7.58</td>
<td>8.26</td>
<td>7.0</td>
<td>7.69</td>
<td>7.17-8.22</td>
</tr>
<tr>
<td>24:1</td>
<td>0.28</td>
<td>0.51</td>
<td>0.32</td>
<td>N/A</td>
<td>0.37</td>
<td>0.25-0.49</td>
</tr>
<tr>
<td>Other</td>
<td>7.32</td>
<td>9.60</td>
<td>9.25</td>
<td>N/A</td>
<td>8.72</td>
<td>7.50-9.95</td>
</tr>
<tr>
<td>Total %Δ3</td>
<td>17.39</td>
<td>18.81</td>
<td>20.66</td>
<td>N/A</td>
<td>18.95</td>
<td>17.31-20.59</td>
</tr>
<tr>
<td>Total %Δ6</td>
<td>8.42</td>
<td>7.89</td>
<td>7.41</td>
<td>N/A</td>
<td>7.91</td>
<td>7.40-8.41</td>
</tr>
</tbody>
</table>
Table 16. Content of selected minerals in homogenate of whole ground *C. maenas* (reported as parts per million or percent of sample). Values for mineral content and mercury levels of whole menhaden are for *Brevoortia tyrannus*; (data for *Brevoortia patronus* were not available) from Scott and Latshaw (1993).

<table>
<thead>
<tr>
<th>Category</th>
<th>GC1</th>
<th>GC 2</th>
<th>GC 3</th>
<th>Menhaden</th>
<th>GC Avg</th>
</tr>
</thead>
<tbody>
<tr>
<td>Calcium (%)</td>
<td>5.74</td>
<td>5.61</td>
<td>5.76</td>
<td>0.98</td>
<td>5.70</td>
</tr>
<tr>
<td>Zinc (ppm)</td>
<td>26.50</td>
<td>29.4</td>
<td>28.2</td>
<td>67</td>
<td>28.03</td>
</tr>
<tr>
<td>Potassium (%)</td>
<td>0.22</td>
<td>0.23</td>
<td>0.229</td>
<td>0.16</td>
<td>0.23</td>
</tr>
<tr>
<td>Hg (ppm)</td>
<td>&lt;0.05</td>
<td>&lt;0.05</td>
<td>&lt;0.05</td>
<td>2</td>
<td>&lt;0.05</td>
</tr>
</tbody>
</table>

Table 17. Amino acid content of green crab homogenate (reported as % relative basis). Values for menhaden were not available, so comparison values (reported as % relative basis) for whole frozen herring, *Clupea harengus* are provided from Haaland and Aarnesen (1988). Starred amino acids are essential to fish in general (these are the same as for chickens), *, and chicks, ξ.

<table>
<thead>
<tr>
<th>Amino Acid</th>
<th>GC1</th>
<th>GC2</th>
<th>GC3</th>
<th>Average</th>
<th>GC±0</th>
<th>Herring</th>
</tr>
</thead>
<tbody>
<tr>
<td>Methionine*</td>
<td>1.30</td>
<td>1.30</td>
<td>1.46</td>
<td>1.36</td>
<td>1.45-1.26</td>
<td>3.00</td>
</tr>
<tr>
<td>Cystine</td>
<td>0.49</td>
<td>0.49</td>
<td>0.49</td>
<td>0.49</td>
<td>0.49-0.49</td>
<td>0.89</td>
</tr>
<tr>
<td>Lysine*</td>
<td>2.93</td>
<td>2.93</td>
<td>3.01</td>
<td>2.95</td>
<td>3.00-2.91</td>
<td>7.61</td>
</tr>
<tr>
<td>Phenylalanine*</td>
<td>2.36</td>
<td>2.44</td>
<td>2.44</td>
<td>2.41</td>
<td>2.46-2.36</td>
<td>3.10</td>
</tr>
<tr>
<td>Leucine*</td>
<td>3.58</td>
<td>3.74</td>
<td>3.82</td>
<td>3.71</td>
<td>3.84-3.59</td>
<td>7.93</td>
</tr>
<tr>
<td>Isoleucine*</td>
<td>2.60</td>
<td>2.60</td>
<td>2.76</td>
<td>2.66</td>
<td>2.75-2.56</td>
<td>4.42</td>
</tr>
<tr>
<td>Threonine*</td>
<td>2.28</td>
<td>2.28</td>
<td>2.28</td>
<td>2.28</td>
<td>2.28-2.28</td>
<td>4.55</td>
</tr>
<tr>
<td>Valine*</td>
<td>6.34</td>
<td>5.53</td>
<td>6.26</td>
<td>6.04</td>
<td>6.49-5.60</td>
<td>0.73</td>
</tr>
<tr>
<td>Histidine*</td>
<td>1.22</td>
<td>1.22</td>
<td>1.22</td>
<td>1.22</td>
<td>1.22-1.22</td>
<td>1.94</td>
</tr>
<tr>
<td>Arginine*</td>
<td>3.66</td>
<td>3.82</td>
<td>3.82</td>
<td>3.77</td>
<td>3.86-3.67</td>
<td>6.34</td>
</tr>
<tr>
<td>Glycine ξ</td>
<td>5.28</td>
<td>5.53</td>
<td>5.37</td>
<td>5.39</td>
<td>5.52-5.27</td>
<td>5.80</td>
</tr>
<tr>
<td>Aspartic Acid</td>
<td>5.93</td>
<td>5.85</td>
<td>5.77</td>
<td>5.85</td>
<td>5.93-5.77</td>
<td>8.68</td>
</tr>
<tr>
<td>Serine ξ</td>
<td>1.87</td>
<td>1.87</td>
<td>1.87</td>
<td>1.87</td>
<td>1.87-1.87</td>
<td>4.08</td>
</tr>
<tr>
<td>Glutamic Acid</td>
<td>10.33</td>
<td>10.08</td>
<td>10.33</td>
<td>10.24</td>
<td>10.38-10.10</td>
<td>12.45</td>
</tr>
<tr>
<td>Proline ξ</td>
<td>3.82</td>
<td>3.66</td>
<td>3.90</td>
<td>3.79</td>
<td>3.92-3.67</td>
<td>N/A</td>
</tr>
<tr>
<td>Hydroxyproline</td>
<td>0.08</td>
<td>0.08</td>
<td>0.08</td>
<td>0.08</td>
<td>0.08-0.08</td>
<td>0.67</td>
</tr>
<tr>
<td>Alanine</td>
<td>3.74</td>
<td>3.82</td>
<td>3.82</td>
<td>3.79</td>
<td>3.84-3.75</td>
<td>6.83</td>
</tr>
<tr>
<td>Tyrosine</td>
<td>2.44</td>
<td>2.36</td>
<td>2.60</td>
<td>2.47</td>
<td>2.59-2.34</td>
<td>2.87</td>
</tr>
<tr>
<td>Tryptophan*</td>
<td>0.16</td>
<td>0.16</td>
<td>0.16</td>
<td>0.16</td>
<td>0.16-0.16</td>
<td>1.07</td>
</tr>
</tbody>
</table>
Discussion

The case for green crab meal as a fishmeal substitute:

Fishmeal is the primary protein in feed formulated for global aquaculture operations, and is the largest variable expenditure in the aquaculture industry (Naylor et al., 2009). Thirty-two percent of world fishmeal production was used for aquaculture in 1999, and this proportion is forecasted to rise to 70% by 2015 (FAO, 1995; 2002). The remainder of the bulk of world fishmeal is used in the production of livestock, notably for poultry and swine (FAO, 2002) but also in fur production (Bimbo et al., 2009).

The biomass of wild-caught forage fish populations (e.g. menhaden, anchovies, sardines, capelin; Naylor et al., 2009) that comprise this fishmeal is highly volatile due to the sensitivity of these populations to cyclical climatic events (eg: El Niño-Southern Oscillation events and hurricanes; Naylor, 2009; Bimbo et al., 2009), which sometimes can negatively affect recruitment, resulting in as much as a doubling in the price of this raw material (Tacon, 2008; McCoy, 1990). In addition, 75% of forage fisheries (sardines, menhaden, etc.) currently are fully exploited or even over-exploited (Tacon, 2008; McCoy, 1990; FAO, 1995; 2002; Bimbo et al., 2009).

Reports commissioned by various authorities have reported that by 2020 existing fishmeal/fish oil resources will no longer be able to support industry demand (FAO, 2002), but others report that fishmeal replacements will rise to meet this demand as forage fish become too expensive to use (Tacon et al., 2008). Much research has gone into developing and testing alternative fishmeal replacements. Previously tested fishmeal protein replacement options (in the model system of the Atlantic cod, Gadus morhua, alone) include soy (Walker et al., 2010), microalgae (Walker and Berlinsky, 2011) and
meal made of Antarctic krill *Euphausia superba* (Karlsen et al., 2006). Another possible fishmeal replacement is the invasive green crab that is an easily-harvested, unexploited, marine protein resource found worldwide in most temperate regions.

Before green crab homogenate (GCH) can be considered for commercial use as a substitute for fishmeal, several requirements must be satisfied. First, GCH composition should be compared to forage fish homogenates (Tables 1-4) to determine optimal test species for a diet containing green crab meal. Whole green crab homogenate resembles the proximate profile of whole menhaden, but is lower in moisture, protein, and fat while having a much higher ash content. Green crab homogenate, therefore, is less valuable per pound in terms of protein or oil content, but also should be less susceptible to bacterial, oxidative, and microbial spoilage than menhaden meal. It is known that whole green crabs spoil more slowly than several other commonly-eaten species of crab (Robson et al., 2006). The discrepancy between the calculated “protein content” (Table 1) of GCH and the “amino acid content” of GCH (Table 4) is explained by the fact that chitin is a long-chain polymer of N-acetylglucosamine, a nitrogenous compound, and protein content is back-calculated from the total nitrogen present in the sample (AOAC, 990.03).

**Processing fish/crab meals:**

Generally, the processing of fishmeal involves several steps, including cooking, pressing, drying, and milling. Cooking coagulates fish proteins and liberates fat and oil. Pressing separates liquids (fat and oil) from solids (ash and protein). A further centrifugation step often speeds the separation of oil and water (FAO, 1986; EPA, 1995). Drying renders the solids (often known as the “press cake”) less available for microbial growth. Sometimes preservatives also are added (eg: ascorbic acid, formaldehyde,
nitrate). Finally, the product is milled to produce standard-sized pieces (FAO, 1986: EPA, 1995). Processing green crab homogenate by the same means would achieve the same end product (a shelf-stable meal). The green crab meal, however, would have different practical uses than regular fishmeal because of its relatively high ash content. It is likely that green crab meal would need less preservative (relative to fish meal) because of its lower oil content, and less input of heat energy (relative to fish meal) due to its relatively lower water content.

**Applications for green crab meal in agri/aquaculture:**

The high concentration of glutamic acid in green crab homogenate suggests that a meal from this product would be an organoleptically appealing product to many carnivorous species of marine animals. In 2006-2007, the largest carnivorous consumers of fishmeal in the global aquaculture industry were shrimp, notably whiteleg shrimp *Litopenaeus vannamei*, (24-27% of fishmeal), various species of marine finfish (18-23% of fishmeal), and Atlantic salmon, *Salmo salar*, and other salmonids (15-17% of fishmeal), followed by several species of trout (6% of fishmeal; IFFO, 2007; Tacon, 2008). Inclusion of crab meal in shrimp diets has been explored in several studies, with findings that it is more effective for post-larval stage shrimp than juveniles (Hertrampf et al., 2000). However, shrimp are not cultured in this area, and shipping green crabs from the east coast of America to Asia (where the majority of shrimp culture is done) would not be economical. Salmonids, although farmed in North America, are not good candidates for fishmeal supplementation with *Carcinus maenas* because whole-crab homogenate has high phosphorus, calcium, and total ash contents relative to those of forage fish (Table 3). Experimental diets for chinook salmon rich in these minerals have
been shown to cause cataracts, nephrocalcinosis, suppressed appetite, a general decline in
growth rates, and increased mortality (Richardson et al., 1985). Therefore, an alternate
(ash-tolerant) species would have to be considered for supplementation with whole green
 crab meal.

Marine finfish aquaculture on the US East Coast, and in particular in New
England, is a promising outlet for green crab meal. If existing infrastructure could be
used for local manufacture of green crab meal, shipping and refrigeration costs for
transport and storage of raw crabs would be minimal.

An emerging species in New England’s aquaculture scene, the Atlantic cod,
*Gadus morhua*, might be an optimal species for testing the efficacy of green crab meal in
maritime finfish diets. In Norway, cod have been cultured extensively (Directorate of
Fisheries, 2007), although those projects are now on the decline.

To a certain extent, the nutritional profile of GCH violates ideal protein theory in
the system of cod (the best foods for animals are those most similar in composition to
their own tissue; Walker, 2009). However, a good test diet should mimic the natural diet
of the animal being cultured, and wild cod prey on a variety of invertebrates, including
crabs (Robichaud et al. 1991). Cod are very efficient in digesting invertebrates, most
likely because chitinases are secreted in the stomach and, to a lesser extent, the intestines,
thus making chitin (and likely, its nitrogen) energetically available to these animals
(Toppe et al. 2005). Cobia, *Rachycentron canadum*, which are cultivated in the southern
US, also possess endogenous chitinases. Cobia also would be a good test model for GCH
inclusion, as it is typical for 78% of wild *R. canadum* gut contents (by weight) to be
crustacea (Fines and Holt, 2010). A third potential species in aquaculture is summer
flounder, *Paralichthys dentatus*, which are produced in New Hampshire and eat a wild diet of which almost a third is crustacea (Latour et al., 2007).

GCH processed into a meal would be a source of complete proteins for most farmed fish, although formulators should ensure that the minimal diet inclusion levels (as a percentage of total protein) are met (Halver and Hardy, 2002). GCH provides almost the same amount of docosahexanoic acid (DHA, 22:6 ω-3) per gram of protein as whole menhaden (Table 15); this is one of the few documented essential fatty acids in cod metabolism (Halver and Hardy, 2002). However, relative to forage fish homogenates, GCH still supplies a much smaller relative lipid content (Table 14). The exact lipid content requirement for the diets of most commercially-raised species of fish is usually assumed to be around ten percent of the dry weight of the diet, which is assumed to spare all protein intake for anabolism (Halver et al., 2002). Lipid only accounts for about 2% of the dry weight of GCH, but separation of solids from liquids during the cooking and pressing stages of processing GCH into meal would allow processors to enrich the meal to the desired fat content by the addition of fat separated from a larger starting volume of GCH. Protein and ash left over as a result of this process could be utilized in some other capacity, perhaps as a fertilizer.

Dietary studies regarding high-ash test diets (and diets including crab byproducts) for cod have shown results indicating that cod generally grow faster with higher calcium and phosphorus inclusion, with a slight decrease in Feed Conversion Ratio at the highest-ash-inclusion end of these test diets (Toppe et al. 2005; Morais et al. 2001). Generally, cod do not develop adverse physical anomalies with high ash inclusion, even though these diets have reduced digestibility (Toppe et al. 2005; Morais et al. 2001).
There also may be terrestrial applications for use of GCH (processed into green crab meal) in New England. It has been shown that fishing industry waste (lobster heads/fish racks/crab waste) is an effective replacement for imported fishmeal in the development of broiler chickens, despite its high ash content (Adesehinwa et al., 2005). Further, laying hens have been supplemented with shells from shelled eggs for decades, with the understanding that thicker shells are accomplished by the ash (Ca\textsuperscript{+\textsc{+}}) added in this process. Fishmeal is an important expense in the laying hen industry, as broiler chicken rations comprise up to 8% fishmeal (Smith, 1991). Chickens are an excellent test market for crab meal because they can self-select for the correct ration of protein if provided with grain and protein food resources (Forbes and Shariatmadari, 1994).

**Conclusion/Future Applications:**

Green crab homogenate has favorable nutritional characteristics for applications in fishmeal replacement. By processes similar to those described previously, GCH could be processed into a green crab meal with similar characteristics to fishmeal. This meal could be used as a fishmeal replacement at several inclusion levels in experimental pelletized diets for ash-tolerant species. Prior to extruded pellet manufacture, diet formulation software (ex: Winfeed or Kasturi) could be used to ensure that all requirements were met in these diets and that they were formulated according to lowest possible ingredient cost. Fish could be fed to satiation on these diets, and also on a control (fishmeal and fish-oil containing) diet. Food intake, accounting for food not consumed as well, should be calculated, with growth being checked by weighting a representative sample of fish from every treatment every week or two weeks, which would allow for adjustment of feed rations. This would continue for a period of months,
at the end of which a representative number of randomly selected fish from each
treatment would be sacrificed and weighted whole. Some of the filets of these fish (in
addition to wild filets from similar-sized fish provided as an additional control) should be
analyzed for proximate composition, fatty acid composition, amino acid composition, and
trace mineral content (with regard to human requirements). The rest of the filets from
each treatment (in addition to wild filets from similar-sized fish provided as an additional
control) should be prepared by the same (regionally-appealing) recipe and offered to a
test group under blinded and consistent conditions (red-light filters, individual booths,
etc) to examine whether experimental filets are distinguishable from wild filets and
whether certain treatments produce more appealing filets than others. The livers of the
sacrificed fish should be weighted for determination of hepatosomatic index (HSI), an
overall indicator of the condition of the animal. In addition, feed conversion ratio (FCR)
should be calculated for experimental fish as mass of food consumed (dry weight)/body
mass gain (dry weight) in order to check the relative efficiency of the different diets. A
similar study would be easy to stage for chickens.

Continuation of this work in the form of one of these studies (in fish or chickens)
should be considered, as green crabs are plentiful and easy to harvest, and could form the
basis of a new fishery in New England. Removing green crabs from New England’s
ecosystems could perform a valuable ecological service and improve the yield of the
area’s other fishing industries via removal of early life-history predators.
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