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CAUSES AND CONSEQUENCES OF INDIVIDUAL PHENOTYPIC DIFFERENCES IN BRACHYURAN CRABS WITH A FOCUS ON BEHAVIOR

By

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ABSTRACT

Individual variation defines almost every morphological, physiological, and behavioral aspect of populations and is a fundamental component of many ecosystem processes. Recent work indicates that accounting for these individual differences can enhance our ability to predict community responses to environmental disturbances which is becoming increasingly important in an era of extraordinary global change. However, our understanding of how different individual characteristics are connected to each other and governed by the environment remains limited.

This study sought to evaluate the relationship between individual behavior, physiological condition, and local habitat for Brachyuran crabs as well as the subsequent strength of their predator-prey interactions within oyster reefs communities. Here, I examined the effects of parasitic infection, diet, habitat quality, season, and conspecific density on crab behavioral traits and physiology. I also evaluated how consistent individual behavioral differences, i.e. personalities, interact with predator type and habitat quality to influence individual mortality and movement patterns. These relationships are essential for calculating population dynamics across multiple spatial scales.

My research found that crab energy stores were strongly dependent upon diet and spawning season. In turn, individual crab activity level and reproductive effort were tied to these energy stores and the local environment. Individuals in structurally degraded oyster reefs would generally exhibit lower activity levels and decreased reproductive output in comparison to crabs which inhabited healthy, structurally complex reefs.

Individual activity was further decreased by reductions in conspecific density, which correlated to habitat quality, and by parasitic infection. Additionally, individual behavior influenced predation risk with bold crabs predominantly consumed by active hunters and shy crabs preferentially selected by ambush predators. Personality also interacted with habitat quality as crabs on low quality reefs rapidly left the region, starting with the boldest individuals; whereas high quality reefs had greater levels of predation, particularly among bold crabs. These findings demonstrate that individual phenotypic variation mediates divergent community interactions across habitat quality and provides several mechanisms through which spatially structured populations may develop.

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CHAPTER 1

INTRODUCTION

One of the greatest challenges for ecologists is to predict the response of ecological communities to environmental change. Towards this end, researchers seek to understand the underlying factors which control the abundance and distributions of species (i.e. community structure). For over 50 years, scientists have recognized that species interactions such as interspecific competition and predator-prey relationships can regulate community structure (Elton 1949, Hairston et al. 1960, Connell 1961, Paine 1966). For instance, Connell (1961) famously used barnacles to demonstrate that species can control the distribution and establishment of other species by outcompeting them for vital resources, while Paine (1966) proved that predatory seastars can likewise govern the species diversity of lower trophic levels by feeding primarily upon the competitively dominant prey species. Scientists have traditionally evaluated the impact species have on communities by using measures of central tendency (e.g. mean values, least squares regression equations) and treating individuals within a population as functionally equivalent and interchangeable (Bennet 1987, Violle et al. 2012). However, in reality, each individual is unique, and ecologists have recently started to acknowledge the importance of phenotypic variation for community dynamics (Bolnick et al. 2011, Violle et al. 2012).

Phenotypic variation is a pervasive feature of wild populations since individuals can differ in their morphology, physiology, and behavior (Chown 2001, Bolnick et al. 2002, Sih et al. 2004). In fact, trait differences between individuals can even surpass mean trait differences between species in some communities (e.g. butterfly wing morphology; Hebert et al. 2004). Individual variation forms the basis of fundamental ecological processes, serving as the raw material for natural selection (Lande 1976) and niche specialization (Roughgarden 1972). Theoretical models investigating the effect of individual differences on population dynamics and interspecific competition have found conflicting results. For example, different models demonstrate that trait variability can decrease or increase population extinction risk depending on the trait and heritability assumed (Fox and Kendall 2002, Lloyd-Smith et al. 2005), while differences in competitive ability can lower or raise equilibrium population densities (Bürger 2005, Kopp and Hermisson 2006). Additionally, recent studies have shown that individual differences may shape community structure by mediating trophic cascades (Keiser et al. 2015), dispersal patterns (Cote and Clobert 2007), disease spread (Keiser et al. 2016), and invasion success (Forsman 2014). Understanding the causes and consequences of phenotypic variation can therefore help scientists mechanistically predict future community dynamics.

My dissertation expands upon our knowledge base by quantifying the relationship between environmental variables and phenotypic differences as well as the effect these differences have on predator-prey interactions. I primarily focus on behavioral differences because behavior modifications are frequently the first organismal response to environmental change; however I also examine key physiological parameters (e.g.

individual energy stores). Here, I use Brachuryan crabs (*Eurypanopeus depressus*, *Callinectes sapidus*, and *Panopeus herbstii*) as model organisms in the North Inlet Estuary, South Carolina. All three of these species commonly inhabit intertidal oyster reefs and saltmarshes along the eastern seaboard of the United States (Gosner 1978, Millikin and Williams 1984, Williams 1984, Kaplan 1988) where they serve as both important consumers and prey to a wide variety of predators (Laughlin 1982, McDonald 1982, Silliman et al. 2004). This dissertation explores four widespread drivers of phenotypic differences in these species and experimentally determines the consequences these differences have in the laboratory and field.

Part I: Causes of phenotypic differences

In Chapter 2, I evaluate the effect an invasive parasite, the rhizocephalan *Loxothylacus panopaei*, has on the metabolism and behavior of *Eurypanopeus depressus*. Parasites are ubiquitous components of natural ecosystems with reviews on parasite prevalence finding that, on average, 30% of host populations are infected by parasites (Torchin et al. 2002, Torchin and Mitchell 2004). As globalization continues, native species are projected to encounter new parasites whereas introduced species are expected to be released from their parasites (Torchin et al. 2002, Robertson et al. 2013). Understanding the full consequences parasites have on individuals is therefore becoming ever more important. Although parasites are well-known to cause host trait modifications (Fritz 1982), research on rhizocephalans has largely concentrated on castration with few studies investigating other host characteristics (Toscano et al. 2014a). My research helps close this knowledge gap by using field surveys and a series of laboratory experiments to assess differences in respiration rates, digestive efficiency, microhabitat use, and activity level between infected and uninfected crabs.

In Chapter 3, I link dietary differences to physiological and behavioral changes in *Callinectes sapidus*. Dietary differences within populations can come from a variety of natural sources ranging from individual variation in search strategies (Tinker et al. 2007) and handling capabilities (Estes et al. 2003) to spatial variation in food availability (Abbas et al. 2011). Additionally, anthropogenic environmental changes are a growing source of diet variation between individuals. These environmental changes include depletion of local prey species through overharvesting (Wiley et al. 2013) and habitat destruction (Reichmuth et al. 2009) as well as include access to novel food sources through the introduction of new species (Rodriguez 2006). In this chapter, I examine a dietary shift from animal to plant tissue associated with habitat degradation from heavy metal pollution (Reichmuth et al. 2009), and conduct a three-month holding experiment to assess how diet quality and quantity influences crab survival, long-term energy stores, reproductive investment, and aggression.

In Chapter 4, I develop our understanding of how habitat quality and season interact with physiological condition to produce consistent behavioral differences (i.e. personalities) in *Panopeus herbstii*. Many ecological studies have demonstrated that animal behavior depends on a number of environmental factors such as temperature (Biro et al. 2010), predator presence (Briffa et al. 2008), and time of day (Dingemanse et al. 2002). Similarly, numerous physiological studies have shown that endogenous factors such as metabolism (Careau et al. 2008) and hunger level (Stocker and Huber 2001, Chapter 3) can govern individual behavior. Theoretical studies have postulated that feedback loops between environmental and physiological variables can lead to the emergence of animal personalities (Biro and Stamps 2008, Dingemanse and Wolf 2010, Wolf and Weissing 2010, Sih et al. 2015). However, empirical studies which examine the simultaneous effect of endogenous and exogenous variables on personality remain limited. Thus, I employ behavioral assays coupled with dissections to quantify the connection between habitat quality, season, short- and long-term energy stores, and individual activity level.

In Chapter 5, I continue to investigate how habitat quality may influence personalities in *Panopeus herbstii* through changes in conspecific density. In this study, I measure the extent that individual activity level remains consistent across isolated and group contexts that are associated with habitat quality. Fluctuations in conspecific density are a common response to environmental change, and while characteristic of changes in habitat quality and food availability (Heck Jr and Wetstone 1977; Levin 1993; Warren et al. 2001; Goode et al. 2005), are also frequently observed in response to changes in season (Hafez 1961), parasite presence (Ebert et al. 2000), and climate (Sæther et al. 2004). While behavioral ecologists have recently become interested in the stability of personalities across different environmental contexts, experiments examining this phenomenon are scarce (Dingemanse and Wolf 2013). I help fill this hole by statistically analyzing the degree that individuals vary in their behavioral plasticity across social context.

Part II: Consequences of phenotypic differences

In Chapter 6, I use *Panopeus herbstii* to study the ecological consequences of the behavioral differences observed in previous chapters. Predator-prey interactions are critical to shaping community structure (Berger et al. 2001, Hawlena and Schmitz 2010), and can mediate trophic cascades directly through the removal of prey (i.e. consumptive effects) and indirectly by inducing behavioral alterations in prey (i.e. non-consumptive effects; Schmitz et al. 2004). Despite advances in our ability to predict the response of prey to predators (Schmitz 2005), the effect prey behavioral differences have on survival in a multi-predator system remains unclear. Here, I conduct laboratory holding experiments to determine the influence personality has on individual survival against two predator species with different hunting strategies.

Finally, in Chapter 7, I examine how habitat quality and personality interact to affect the life history traits of *Panopeus herbstii* in the natural environment. Although animal personalities are increasingly recognized as an influential factor in shaping species interactions and population dynamics (Cote et al. 2010, Dingemanse and Wolf 2010, Pennisi 2016, Chapter 6), the relative importance of personalities in comparison to other environmental parameters is unknown. This lack of information is further compounded by a dearth of field-based studies of personality that cover multiple environmental contexts (Wolf and Weissing 2012, Dall and Griffith 2014). Therefore, I conduct a caging experiment and reciprocal transplant experiment across low and high quality reefs to determine the extent that personalities impact crab survival and migration patterns in the wild.

CHAPTER 2

RHIZOCEPHALAN INFECTION MODIFIES HOST FOOD CONSUMPTION BY REDUCING HOST ACTIVITY LEVELS[1]

ABSTRACT

Although castration by rhizocephalans on crab species is well documented, the accompanying effects of infection on behavior and metabolism have remained relatively unstudied. In this investigation, we examined flat back mud crab (*Eurypanopeus depressus*) physiology and behavior in an attempt to elucidate why infected crabs exhibit a previously documented reduced functional response. Crab respiration and digestion rates were analyzed to determine if infection altered metabolic rate. Laboratory behavioral experiments and a field survey were conducted to determine how infection alters crab feeding behavior and activity levels. Although we found no statistical difference between infected and uninfected crab metabolic or digestive rates, we discovered that, both in the lab and in the field, infected crabs exhibited substantially altered behavior. In the laboratory infected crabs reacted nearly 3 times slower to the presence of prey and spent over 22% more of their time hiding, whereas uninfected crabs were significantly more active. During field sampling, infected crabs were significantly more likely to be found hiding within empty oyster shells while uninfected crabs spent more time in the exposed positions of the habitat. We conclude that rhizocephalans can

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reduce the host functional response by altering host behavior. Here, these induced changes can impact community structure by altering trophic interactions so that infected crabs spend less time foraging and more time hiding, potentially reducing their predation risk.

INTRODUCTION

Parasites are well known for manipulating host behavior (Belgrad and Smith 2014, Hindsbo 1972, Moore 2002, Poulin 1995, Poulin 2010). Classical examples include acanthocephalans altering amphipod phototactic behavior to increase their predation risk by mallard ducks (Bethel and Holmes 1973, Bethel and Holmes 1977) and the trematode *Dicrocoelium dendriticum* inducing infected ants to climb blades of grass consumed by sheep (Carney 1969). Other common host behaviors modified by parasites include foraging behavior (Koella et al. 1998), sexual behavior (Dunlap and Schall 1995, Vance 1996), activity levels (Moore 2002, Webster 1994), and habitat selection (Belgrad and Smith 2014, MacNeil et al. 2003).

Such changes to behavior are significant because they directly impact host fitness (Fitze et al. 2004, Marzal et al. 2005, Yanoviak et al. 2008) and indirectly influence community structure (Minchella and Scott 1991, Mouritsen and Poulin 2005). For example, killifish infected by trematodes more frequently exhibit conspicuous behaviors such as jerking motions, and are subsequently more susceptible to predation from birds (Lafferty and Morris 1996). Correspondingly, isopods infected with acanthocephalans are more active and frequent light-colored exposed substrates more than uninfected isopods, and subsequently infected isopods were preferentially consumed by starlings in the laboratory (Moore 1983). Behavioral changes induced by parasites can impact community structure by altering trophic interactions either through manipulating the host functional response (Toscano et al. 2014a, Wood et al. 2007) or the hosts' predation risk (Minchella and Scott1991).

One type of parasite recognized for altering decapod host sexual behavior and population dynamics is the rhizocephalan barnacle (Mouritsen and Poulin 2002, Reinhard 1956, Sloan, 1984). Rhizocephalans are extremely well-adapted cirripeds, which solely require crustaceans, principally crabs, as hosts (Hoeg 1995). Parasitic infection begins when a female cyprid larva settles on either a male or female crab and grows a system of branching roots along the intestines of the crab. This initial stage, called the interna, resides entirely within the host (Alvarez et al. 1995, O'Brien and Van Wyk 1985, Walker et al. 1992). Eventually an externa is produced as the rhizocephalan matures, and a portion of the parasite erupts under the abdomen of the crab. The externa comprises the reproductive body of the parasite and resides in the same location that normally would be occupied by the egg mass of an uninfected brooding female decapod. The externa will remain a small bud until a male cyprid larva fertilizes the externa (O'Brien and Van Wyk 1985). In addition to castration for both male and female crabs, rhizocephalans produce a variety of effects in their hosts, ranging from reduced growth rates (O'Brien and Van Wyk 1985) to altered aggression (Innocenti et al. 2003) and burrowing behavior (Innocenti et al. 1998, Mouritsen and Jensen 2006).

The invasive rhizocephalan barnacle, *Loxothylacus panopaei*, infects and castrates the flat-backed mud crab, *Eurypanopeus depressus*, and other xanthid crabs along the Atlantic coast of North America (Alvarez et al. 1995). Originally a native of the Gulf of Mexico, *L. panopaei* began to invade the eastern coast of the United States in 1964, presumably through the importation of oysters from the Gulf of Mexico, which likely bore infected crabs (Van Engel et al. 1966). The rhizocephalan has a prevalence of between 8% and 29%, depending on the month, within North Inlet estuary in South Carolina (O'Shaughnessy et al. 2014, Toscano et al. 2014a), but can reach as high as 90% in its introduced range (Hines et al. 1997, Kruse and Hare 2007). Recently, Toscano et al. (2014) found that mature *L. panopaei* reduces the functional response of *E. depressus*, limiting the amount of mussels the crab consumes. In contrast, some studies on animal feeding behavior found that parasitized hosts often increased their consumption (Barber et al. 2000, Koella et al. 1998). Similarly, infected crabs may also be expected to consume more mussels to meet the increased energetic demands associated with supporting such an intrusive parasite. We therefore sought to determine what underlying factors caused infected *E. depressus* to exhibit a reduced functional response.

Several mechanisms could potentially explain the decreased consumption by infected crabs. First we hypothesized that decreased mussel consumption by crabs could be the product of a reduced metabolic rate (i.e., decreased energy needs), which could occur if rhizocephalans reduce host energy expenditures on growth or movement. Second, rhizocephalans may decrease the digestive rate (i.e., decreased food processing capability) of crabs since the parasite interna infests the crab body and may be damaging or reducing the efficiency of the digestive tract. Third, rhizocephalans may indirectly lower the consumption rates of their hosts by altering crab behavior to be less active in finding prey or to increase the reaction time of crabs to the presence of prey. Such behavioral changes can potentially reduce the functional response of the host by decreasing crab foraging time or lowering the frequency with which the crab encounters mussels.

In the present study, we measured the metabolic and digestive rates of infected and uninfected crabs in the laboratory to determine the influence of parasitic infection on these processes. We then conducted a series of observational studies to quantify crab activity levels and reaction time to the presence of mussels. Finally, we conducted a field survey to assess the microhabitat preferences of infected and uninfected crabs.

METHODS

Sampling

Eurypanopeus depressus were collected from oyster reefs within the North Inlet Estuary (33°20′N, 79°10′W, Georgetown, South Carolina) 24 h prior to experimentation. All oyster reefs were within 5 km of each other, and no oyster reef was closer than 200 m to another sampled reef. Infected crabs were identified by the presence of parasite externae, which signifies the parasite was mature (Alvarez et al. 1995). We only used infected crabs with a single mature externa to reduce any variation produced by multiple infections. Our sampling methods could not discern whether crabs were infected with the immature, internal phase of the parasite, so it is possible that some crabs categorized as "not infected" did have infections. We utilized male and female crabs in both infected and uninfected treatments because the effects of parasitic castration made distinguishing the sex of infected crabs difficult (Daugherty 1969), and gender was not found to have an effect on any of the crab response variables (six separate generalized linear models $P > 0.28$). Therefore, crabs of both genders were grouped for the remainder of the analyses. We sampled and studied 160 infected and 160 uninfected crabs (carapace width

8–14 mm for both infected and uninfected crabs) between July 5 and August 15, 2013. Crabs were starved 24 h prior to experimentation to standardize hunger levels and were monitored for 24 h after their respective experiments to ensure none underwent ecdysis or extruded eggs. Each crab was used only once over the course of an experiment, and no crabs were used in multiple experiments. Scorched mussels, *Brachidontes exustus,* are an important prey item of *E. depressus* (McDonald 1982, Toscano et al. 2014a) and were collected from the same reefs from which we sampled crabs (shell length 3.5–7.5 mm).

Metabolism

We determined whether parasitic infection reduced the metabolic rate of *E. depressus* by measuring the oxygen consumption rate of infected and uninfected *E. depressus* inside hermetically sealed individual plastic containers (20 × 12 × 11 cm). Filtered seawater (salinity 32–34 psu, temperature 24.3 ± 0.8 °C, 1 μm filter) was collected from North Inlet. Containers were set on a stirring plate and compartmentalized with plastic mesh in cylindrical form (diameter 12 cm, height 11 cm, pore size 0.5 cm). A magnetic stirrer was placed in one compartment to ensure all dissolved oxygen (DO) was distributed evenly within the container. The other compartment received either a single infected crab, uninfected crab, or no crab (control) depending on the treatment. Each trial had two replicates of each treatment, with five trials run over three consecutive days (n = 10 for each treatment). Trials lasted 1 h with a 10 min acclimation period beforehand to help reduce the effect of handling. Concentration of DO was measured every 10 min using a microprocessor dissolved oxygen meter with a Clark-type electrode (Hanna Instruments, HI 9146 N).

Individual crab metabolic rates were calculated by taking the average change in DO concentration between the 10 min intervals, standardized by container water volume and crab weight, then corrected for changes in oxygen consumption not attributable to crabs and/or the parasite by subtracting the average difference in DO consumption calculated from the control containers within the same trial. All statistical analyses were done in R, version 3.0.1 (R Development Core Team, Auckland, New Zealand). A Shapiro–Wilk test indicated that the data were not normally distributed. We therefore compared oxygen consumption between infected and uninfected crabs using a Wilcoxon rank sum test with continuity correction.

Digestion

We conducted observational studies to determine if reduced rates of mussel consumption reported for infected crabs could be attributable to slowed digestion rates, measured as gut passage time. Crabs collected from the North Inlet Estuary (carapace width = 9–13.5 mm) were starved for 24 h to ensure empty guts (Hill 1976, Wolcott and Wolcott 1987, personal observations) before being placed in individual cylindrical glass containers (height 5 cm, radius 3 cm) filled with seawater and allowed to acclimate for 5 min. After acclimation, a crushed mussel (shell length = 4–7 mm) was placed in the center of the container. We continuously observed the crabs for 1 h to determine when mussel consumption began and ended. After 1 h, crabs were checked every 10 min until they produced feces. Each trial had five infected and uninfected crabs with six trials run over six consecutive days (n = 30 for each treatment). Gut passage time was calculated as the time from initial food consumption to the time the crab first produced feces. We used a mixed-effects generalized linear model (GLM) with an exponential distribution to test the fixed effects of infection status and crab wet weight (g) as well as the random effect of trial on crab gut passage time. To determine if trial had a significant influence on gut passage time, we ran a chi-square test comparing a model with trial as a random effect and a model with data pooled across trials.

Laboratory behavioral experiment

We conducted two separate observational studies in the laboratory to determine how parasitic infection of *E. depressus* influences crab feeding behavior and activity level. The first study evaluated the amount of time infected and uninfected crabs spent either feeding, moving, resting, or hiding under shelter. Feeding behavior was defined as the crab actively consuming mussels, while moving behavior was the crab walking or waving its chelipeds. Conversely, a crab was noted as resting when visible and immobile and hiding when not readily visible. Behavioral experiments were run within individual plastic containers (length 15 cm × width 13 cm × height 7.6 cm) filled with continuous running seawater from North Inlet and four cleaned oyster shells (shell length 7.5–11 cm) to provide shelter. Each container had 10 mussels (shell length 3.5–7.5 mm) placed on a cleaned oyster shell 6 h prior to the experiment, allowing mussels time to attach to the shell surface. Depending on the treatment, either a single infected or uninfected crab (carapace width 8–14 mm) was placed in the container and allowed to acclimate for 10 min. Five replicates were run for each trial with five trials conducted over consecutive days (n = 25).

Crabs were observed at night under red light to minimize disturbance and to ensure that crabs were at their most active (Griffen et al. 2012). Crabs were checked every 9 min for 3 h, yielding a total of 20 observations. At each observation, their behavior was noted, and time spent in each behavior was expressed as the proportion of these 20 observations. Feeding and moving behavior were grouped under the category “active,” while resting and hiding behavior were categorized as “inactive” for statistical analysis. As a second metric of crab activity level, we also analyzed the number of times behavior type changed between adjacent observations over the 3-h experimental period. There were no differences in either of these statistics across trials ($P > 0.4$). We therefore pooled the data, allowing us to compare activity level and frequency of behavior changes between infected and uninfected crabs using separate Student t-tests.

Crab reaction time

Our second laboratory study sought to determine if infected crabs responded to the presence of mussels more slowly than uninfected crabs. Crabs were placed in individual cylindrical glass containers (height 5 cm, radius 3 cm) and allowed to acclimate for 5 min. Following the acclimation period, we introduced a single mussel into each container and recorded the amount of time (min) taken for the crab to begin manipulating the mussel. To reduce variations in reaction time brought about by differences in the crab:mussel size ratio, we matched larger crabs to larger mussels (crab carapace width = 8–14 mm; mussel shell length = 3.5–6 mm). Five infected and uninfected crabs per trial were observed at night under red light for a maximum of 6 h, with seven trials conducted over seven consecutive days ($n = 35$). We pooled the data as reaction times did not differ for either infected or uninfected crabs across trials (two one-way ANOVAs, $P > 0.05$). Some of the crabs did not react to the presence of mussels by the conclusion of the experiment, so we conducted Cox's proportional hazards analysis (R Package *survival* v. 2.37-7) to compare the overall reaction time of infected and uninfected crabs, allowing us to right censor the data. A Cox proportional hazards analysis is a statistical model which recognizes that some of the highest values in an experiment are simply the maximum possible value because an event did not occur by the end of the observation period (i.e., the data are right censored), so the model weighs the data points accordingly. One uninfected crab was excluded from the analysis because during the observational period the crab underwent ecdysis.

Field behavioral survey

Laboratory observations found that infected crabs tend to hide within empty oyster shells (see results). We therefore surveyed where infected and uninfected crabs are found within oyster clusters to evaluate whether differences in behavior between infected and uninfected crabs expressed themselves in the field. We collected crabs haphazardly from intertidal oyster reefs in North Inlet Estuary (carapace width = 8–14 mm). We sampled over a 10-day period, collecting the first six infected and uninfected *E. depressus* encountered on each day. We spread our sampling effort out over several days in this manner in order to capture a wide range of environmental variation associated with weather conditions and tidal cycles that varied daily (air temperature 25.1–30.7 °C, time from high tide 221–282 min). For each collected crab, we categorized the location as either hiding (within empty oyster shells) or exposed (outside empty oyster shells) (n = 60). All crabs which were categorized as exposed were within a couple body lengths of an empty oyster, but due to the rapid movement of crabs and the complexity of the reef, we were unable to quantify the initial distance individual crabs were from a refuge. We recorded the air temperature (°C) and time from high tide (min) for each sampling period and analyzed the data using a GLM with a binomial distribution to determine if air temperature, time from low tide, carapace width, or infection status had a significant effect on crab location.

RESULTS

Metabolism

The mean ± SE respiration rate of infected crabs was 0.66 ± 0.28 μl O_2/h/g crab tissue while uninfected crabs respired at a rate of 0.22 ± 0.05 μl O_2/h/g crab tissue. Although the mean respiration rate of infected crabs was almost a three-fold increase over uninfected crabs, this difference was not significant (Wilcoxon rank sum test, W = 62.50, *P* = 0.364).

Digestion

We found that neither parasitic infection nor crab size significantly altered gut passage time (mixed-effects GLM, t = −0.62, *P* = 0.538 and t = −1.327, *P* = 0.185, respectively; Figure 2.1), while the random effect of trial (day #) caused substantial variation in gut passage time (Chi-square = 15.33, df = 5, *P* = 0.009).

Laboratory behavioral experiment

Infected crabs were significantly less active than uninfected crabs (t-test, t = −3.50, df = 36.02, *P* = 0.001).While infected crabs were active during 6.8 ± 1.6% of the 3-h observational period, uninfected crabs were active 19 ± 3.1% of the time, a 2.8-fold increase (Figure 2.2). Parasite infection also reduced the frequency with which crabs changed their behavior type by 60%, with uninfected crabs altering behavior 10.3 ± 0.7 times per observational period and infected crabs switching behaviors 6.5 ± 0.8 times (t = −3.60, df = 45.45, *P* < 0.001).

We found that infected and uninfected crabs showed substantially different behavior patterns (Figure 2.2). Infected crabs exhibited a nearly five-fold decrease in feeding behavior and more than two-fold time decrease in moving behavior as well as a 20% increase in hiding behavior over that of uninfected crabs. The proportion of time spent either hiding or resting varied widely among individuals for both infected and uninfected crabs, ranging from 10% to 100%. However, only infected individuals spent 100% of the time hiding. Crabs spent the least amount of time feeding, regardless of infection status, and this was the only type of behavior not exhibited by all individuals. Only three infected crabs (12%) and nine uninfected crabs (36%) consumed mussels over the entire experiment and no crabs fed longer than 35% of the observational period.

Crab reaction time

The reaction time of crabs responding to the presence of mussels was approximately a three-fold increase in latency for infected crabs (146.2 ± 24.4 min) than for uninfected crabs (49.6 ± 14.7 min; Cox's proportional hazards, $Z = -3.83$, $P < 0.001$). Although only one uninfected crab did not respond to the presence of mussels during the 6-h observational periods, 10 infected crabs did not respond by the conclusion of the experiment.

Field behavioral survey

Infection status and carapace width had a significant influence on whether we found crabs exposed or hiding within oyster reefs. Specifically, infected crabs were more likely than uninfected crabs to be hiding within empty oyster shells, while larger crabs tended to expose themselves on the outside of oysters (GLM, $t = -3.480$, $P < 0.001$; $t = 2.266$, $P = 0.0253$, respectively; Figure 2.3) with no interaction between infection status and crab width (GLM, SE = 0.33, t = −0.21, *P* = 0.832). Neither air temperature nor time from low tide influenced crab location (GLM, SE = 0.14, t = −0.23, *P* = 0.818; SE = 0.01, t = 0.58, *P* = 0.564, respectively).

DISCUSSION

The parasite-induced reduction in functional response of *Eurypanopeus depressus* does not appear to be a consequence of a decrease in metabolism or digestive efficiency. Instead, the rhizocephalan seems to lower the feeding rate of crabs by altering their behavior so they are less active and spend more time hiding within oysters, effectively reducing the amount of time crabs spend foraging. Reduced host activity levels from parasitic infection have been documented in a number of species (Poulin 1995). For instance, copepods infected with procercoids (larval tapeworms) exhibited lowered motility and a gradual decrease in feeding rate after infection (Pasternak et al. 1995), while trematode infections in marine snails reduced host activity by decreasing the distance infected snails traveled (Miller and Poulin 2001, O'Dwyer et al. 2014, Williams and Ellis 1975). However, decreased host activity levels and changes in host microhabitat preference have not previously been documented in response to rhizocephalan infection.

Potential mechanisms through which the rhizocephalan reduces crab activity include impairing the mobility of the crab or exhausting the host energy stores. These two mechanisms may also interact to raise the cost of movement, which would be expressed as an increase in the active metabolic rate of infected crabs relative to uninfected crabs. Such a cost may further stimulate infected crabs to remain inactive, although we did not test this hypothesis since we measured only resting metabolic rates. The presence of the rhizocephalan externa could limit the mobility of its host by restricting movement or by acting as a cumbersome weight. The externa is similar in shape and relative size to encrusting epibionts such as barnacles which have been known to retard the movement of periwinkles (Buschbaum and Reise 1999) and horseshoe crabs (Overstreet 1983). However, a study comparing the non-brooding behavior of gravid and non-gravid female crabs observed more locomotor activity in brooding than non-brooding females (Ruiz-Tagle et al. 2002), which implies the mass of the externa is not the sole cause for the reduced activity of infected crabs. Rhizocephalans can hypothetically deplete host energy stores by utilizing the energy for its own growth or by causing the host to invest energy into an immune response. Reduced growth rates have been frequently observed in numerous species of crabs infected by rhizocephalans (Hawkes et al. 1987, O'Brien and Van Wyk 1985, Takahashi and Matsuura 1994) which are indicative of depleted host energy reserves, and Robles et al. (2002) found that the rhizocephalan *Loxothylacus texanus* increased the oxygen consumption of the swimming crab *Callinectes rathbunae*. The hemolymph of king crabs infected with rhizocephalans was also found to have elevated hemocyanin and glucose concentrations, suggesting higher energy expenditure, but hemocyte counts remained the same between uninfected and infected crabs, suggesting the immune response was minimal (Shirley et al. 1986).

The rhizocephalan may also reduce crab foraging by impairing the ability of crabs to detect prey. Infected crabs took substantially longer than uninfected crabs to react to prey in both our experiments and those of Toscano et al. (2014a), which can be indicative of decreased sensory perception (Sandahl et al. 2007). Infections by rhizocephalans are known to damage the nervous system of their hosts as the interna rootlets penetrate the thoracic ganglion and ventral nerve cord (Neilson 1970). However, rhizocephalans are unlikely to decrease the olfactory capabilities of crabs since DeVries et al. (1989) determined that crabs infected by *Loxothylacus panopei* had an enhanced sensitivity to peptide pheromones. The increased latency in crab reaction time is more likely to be the consequence of a decrease in crab mobility, especially because the thoracic ganglion is associated with thoracic flexor muscles (Stephens 1986).

Our study did not find a significant difference in metabolism between infected and uninfected crabs unlike Robles et al. (2002). This is likely a product of insufficient replication (n = 10) at the high level of individual variation we observed among crabs. A power analysis determined that more than double the number of replicates would be needed to detect a significant difference given the observed effect size and level of variation seen in crab metabolism. While not significantly different, the higher mean respiration rate of infected crabs compared to uninfected crabs is in the opposite direction than would be required to explain the reduction in functional response that was observed by Toscano et al. (2014a). However, because only short-term, resting metabolic rates of crabs were measured and the rhizocephalan alters crab behavior to be less active, the metabolic demands of infected crabs may be lower than uninfected crabs over the long term. Additionally, our study could not differentiate between parasite and host respiration because completely removing the rhizocephalan kills the crab. Nevertheless, any metabolic needs of the rhizocephalan would have ultimately been fueled by its host as rhizocephalans lack both a mouth and gut, absorbing required nutrients from the host's tissues (O'Brien and Van Wyk 1985).

In both the laboratory and field, infected crabs were more likely to be found hiding within oysters rather than exposed like uninfected crabs. Although smaller crabs were also more likely to hide, carapace length did not interact with infection status, so the behavior exhibited by infected crabs is unlikely to be a consequence of crab size. Our field survey could not differentiate between previously exposed crabs and crabs which may have crawled out of hiding due to our sampling.

In the mud crab, *Panopeus herbstii*, that co-occurs in the same oyster reefs as our study organism, oyster refuge use is inversely related to crab size and increases in response to predatory toadfish cues (Griffen et al. 2012). Smaller crabs are also known to lower their activity in the presence of predator cues while larger crabs remain unresponsive to the cue (Toscano and Griffen 2014). Therefore, the hiding behavior seen in our infected crabs may likely be a predator avoidance response to reduce crab predation risk. This potentially benefits the rhizocephalan since increased host survival would enhance the probability that the parasite can reproduce. Unlike trophically transmitted parasites with multiple hosts (e.g., trematodes), which are commonly known to alter host behavior to increase host predation risk and presumably enhance parasite transmission (Bernot 2003, Levri and Lively 1996), rhizocephalans infect only one host and thus rely on the survival of the host to produce offspring. Consequently, the modified habitat selection of infected crabs has implications for both crab predator–prey interactions and rhizocephalan population dynamics.

Alternatively, crab survival may be decreased due to starvation because the increased hiding time substantially reduces crab foraging (O'Shaughnessy et al. 2014, Toscano et al. 2014a). However, as mentioned previously, the reduction in crab activity potentially decreases metabolic demands, which could offset starvation. Krause et al. (1998) determined that size has a confounding effect on the benefit gained from hiding as smaller fish were subject to higher predation risk when exposed but also were more susceptible to starvation than larger fish. Future studies should therefore encompass the effects that hiding has on foraging time, metabolism, and predation risk in order to determine the full impact that hiding behavior has on crab survival.

Crab infection status was determined by the presence of parasite externae, and we were unable to verify the existence of the parasite interna in dissections of crabs which did not have an externa. Thus, we could not determine the prevalence of crabs in the immature phase of infection. If crabs in the immature phase of infection also exhibited decreased activity levels similar to crabs in the mature infection phase, then our labeling of these crabs as “uninfected” would reduce the difference in activity between infected and uninfected crabs. Consequently, our findings are a conservative assessment of the effects of rhizocephalans on crab behavior.

In summary, rhizocephalans produce a wide variety of effects in their hosts, some of which alter the host's trophic interactions. Our study reveals that rhizocephalans dramatically reduce crab activity, which can influence other types of behaviors and may indirectly affect predator–prey relationships. In order to adequately assess the full effects of parasitic castrators, future research should examine both behavioral and physiological consequences of infection. However, more work is required to understand how different behaviors impact trophic interactions to determine the extent that behavioral modifications resulting from parasite infection alter community dynamics.

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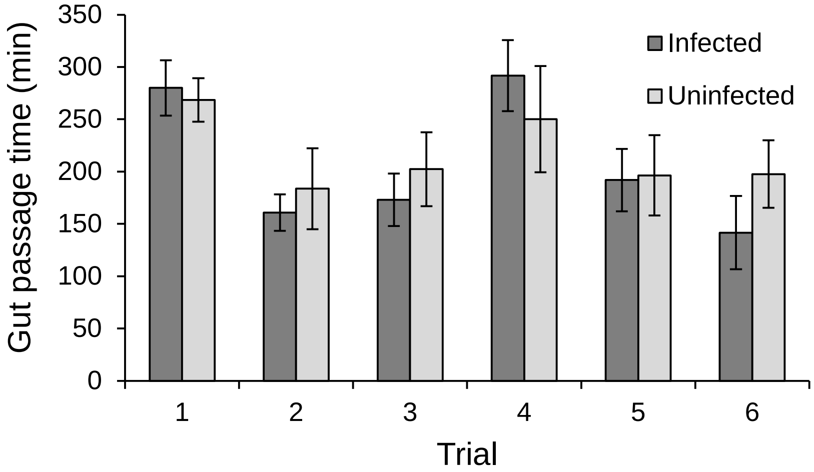

Figure 2.1 Mean (±SE) gut passage time (min) of *Eurypanopeus depressus* infected with the parasite *Loxothylacus panopaei* as well as the gut passage time of uninfected crabs across blocked trials (n=5). Crabs (carapace width 8–14 mm) were collected from the estuary North Inlet between August 3rd and August 9th, 2013.

Figure 2.2 Mean (±SE) percent of time spent either feeding, moving, resting, or hiding by both *Eurypanopeus depressus* infected with the parasite *Loxothylacus panopaei* and uninfected crabs (n = 25). Feeding and moving behavior were grouped as “active” while resting and hiding behavior were grouped as “inactive” for statistical analysis. Crabs (carapace width 8–14 mm) were collected from the estuary North Inlet between July 10th and July 15th, 2013.

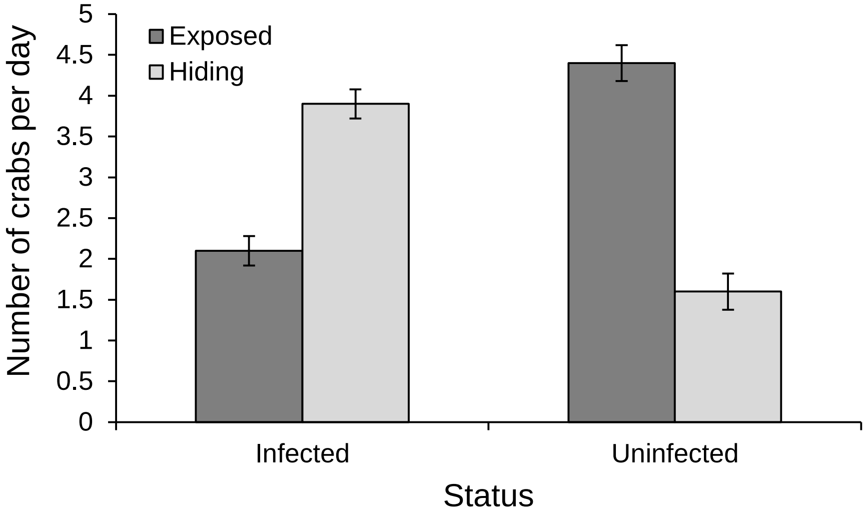

Figure 2.3 Mean (±SE) number of infected and uninfected *Eurypanopeus depressus* found each day in oyster reefs either exposed or hiding (n = 10). Infected crabs hosted the rhizocephalan *Loxothylacus panopaei*. Crabs (carapace width 8–14 mm) were sampled from the estuary North Inlet between August 3rd and August 15th, 2013.

CHAPTER 3

THE INFLUENCE OF DIET COMPOSITION ON FITNESS OF THE BLUE CRAB, *CALLINECTES SAPIDUS*[2]

ABSTRACT

The physiological condition and fecundity of an organism is frequently controlled by diet. As changes in environmental conditions often cause organisms to alter their foraging behavior, a comprehensive understanding of how diet influences the fitness of an individual is central to predicting the effect of environmental change on population dynamics. We experimentally manipulated the diet of the economically and ecologically important blue crab, *Callinectes sapidus*, to approximate the effects of a dietary shift from primarily animal to plant tissue, a phenomenon commonly documented in crabs. Crabs whose diet consisted exclusively of animal tissue had markedly lower mortality and consumed substantially more food than crabs whose diet consisted exclusively of seaweed. The quantity of food consumed had a significant positive influence on reproductive effort and long-term energy stores. Additionally, seaweed diets produced a three-fold decrease in hepatopancreas lipid content and a simultaneous two-fold increase in crab aggression when compared to an animal diet. Our results reveal that the consumption of animal tissue substantially enhanced *C. sapidus* fitness and suggest that

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[2] Belgrad, B.A. and B.D. Griffen. *PLOS One*. 11: e0145481.
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a dietary shift to plant tissue may reduce crab population growth by decreasing fecundity as well as increasing mortality. This study has implications for *C. sapidus* fisheries.

INTRODUCTION

Numerous studies have found that individual diet and physiological well-being are interdependent. Diet plays a crucial role in the metabolic efficiency (Carew et al. 1964, Karowe and Martin 1989) and homeostasis of an organism (Zhang et al. 2009). Diet can also influence the accumulation and toxicity of heavy metals (Peraza et al. 1998, Saric et al. 2002) and even affect the longevity (Bishop and Guarente 2007, Mair and Dillin 2008) as well as the reproductive output of individuals (Xu et al. 1994, Jorgensen and Toft 1997). Shifts in diet may therefore indirectly alter population dynamics by changing an individual's longevity or offspring production. Indeed, dietary alterations have been proposed as the mechanism behind the population decline of some species of seabirds (Kitaysky et al. 2006, Norris et al. 2007) and shore crabs (Griffen et al. 2011), and for fluctuations in the abundance of trout (Kelly and Dick 2005).

Organisms may alter their diet for a variety of reasons. Ontogenetic dietary shifts are a widespread phenomenon (Lucifora et al. 2009, Davis et al. 2011). Mature individuals frequently consume different prey than juveniles due to developmental changes which produce differences in size, competitive ability, and metabolic processes (Lucifora et al. 2009). Diets may also shift in response to alterations in the environment. For instance, seasonal changes (Rosalino et al. 2005), climatic regime shifts (Decker et al. 1995, Kitaysky et al. 2006), and species invasions (Eagles-Smith 2008, Griffen et al. 2008) can induce diet shifts either by introducing new species to consume or by altering the availability of native species. Diseases too can cause dietary shifts either by reducing the abundance of prey species (Moleon et al. 2009) or by impairing the ability of the host to digest or capture prey (Shields 2011). Finally, pollution can cause dietary shifts by altering consumer behavior and/or reducing foraging capabilities. One such example has been found in the blue crab, *Callinectes sapidus* (Reichmuth et al. 2009).

Normally the diet of blue crabs consists of 20–40% mollusks, 10–26% arthropods, 5–12% fishes, and 1–7% polychaetes (Laughlin 1982, Hines 2007, Reichmuth et al. 2009). Algae, sediment, and detritus can also compose a small percentage (~3%) of the diet under normal conditions (Laughlin 1982, Hines 2007, Reichmuth et al. 2009). However, crabs within estuaries contaminated with metals predominantly consume plant matter/algae (27%) and sediment/detritus (39%), and much less animal tissue overall (34%); presumably because of impaired coordination and reduced ability to capture active prey (e.g. fish; Reichmuth et al. 2009). Metal pollution also reduces overall food consumption and causes crabs to exhibit more cannibalistic tendencies as well as abnormally aggressive behavior (Reichmuth et al. 2009, Reichmuth et al. 2011). Specific diets of individual crabs may also be influenced by numerous other factors, including food availability (Blundon and Kennedy 1982), individual preference (Micheli 1995), crab size (Arnold 1984), or physiological condition (Hines 2007).

Blue crabs are a commercially important species which inhabit estuaries in the western Atlantic and can occur from Nova Scotia to northern Argentina (Williams 1974, Millikin and Williams 1984). The species has been harvested by commercial fisheries since the late 19th century and today constitutes a multimillion dollar industry, becoming the largest crab fishery (by pound) in the United States (Rathbun 1884, Rathbun 1887, NMFS 2013). Blue crabs are also an ecologically important species. They consume a wide variety of organisms across several phyla and also act as prey for more than 100 species (Laughlin 1982, Hines 2007). Their predatory activities can have far-reaching consequences as fluctuations in bivalve mortality rates often coincide with blue crab abundance (Fiorenza 1999), and predation by blue crabs can control the structure of benthic infaunal communities (Virnstein 1977). Thus, the impacts of diet selection in this species on individual physiological performance and on fecundity can have important economic and ecological implications.

The purpose of this study was to investigate the relationship between diet, physiological condition, fecundity, and behavior in the blue crab, *C. sapidus*, in order to understand the importance of diet selection for blue crab population dynamics. We therefore experimentally manipulated the diet of crabs both qualitatively and quantitatively and measured resulting differences on crab mortality, reproductive potential (amount of tissue invested in reproduction and egg size), long-term energy stores (hepatopancreas size and lipid content), and aggression. Blue crabs were expected to have reduced reproductive potential and decreased energy stores from consuming seaweed diets since the crabs normally consume animal tissue primarily, while aggression was expected to increase with enhanced hunger levels.

METHODS

Sampling and holding

We collected 60 mature female *Callinectes sapidus* (mean ± SD carapace width = 14.5 ± 0.8 cm) that were not missing any limbs using baited crab traps from the North Inlet National Estuarine Research Reserve (33°20’N, 79°10’W, Georgetown, South

Carolina). Field collections of blue crabs were conducted under a permit issued by the South Carolina Department of Natural Resources, and blue crabs are not an endangered species. Crabs were obtained during early May 2014 over the course of a week, one month prior to the peak spawning season (Dickinson et al. 2006, Darnell et al. 2009). We started the experiment in blocks (five total) as crabs were captured so that no crabs were held longer than 24 hours before commencing the study and being fed.

Crabs were transported to the Baruch Institute wet lab (situated on North Inlet) where they were placed into individual plastic containers (length 29.8 cm, width 19.7 cm, height 20.3 cm)submersed within seven flow-through tanks supplied with seawater directly from North Inlet. Water temperature matched environmental conditions and varied between 25.4–34.5°C throughout the experiment. Individual containers were filled with a 1.5 cm layer of sediment collected from the field and continuously received water at a rate of ~1.3 L/min. Once a week the containers were cleaned with an aquarium vacuum and the substrate layer was replenished with new sediment. This sediment was provided because sediment is required for development of normal egg masses in this species (Zmora et al. 2005). Sediment may also have served as an additional source of food, though sediment consumption was not measured. Crabs that died before the end of the experiment were frozen and stored at -20°C for later dissection. Any egg masses produced by the crabs were stored in the freezer for later analyses. The experiment was terminated after 12 weeks, on July 13, 2014 when surviving crabs were frozen for later dissection. No molting occurred during the course of this study and no crabs died or produced broods until over two weeks after the experiment began.

Feeding

Throughout the duration of the experiment, crabs were fed either exclusively ribbed mussels (*Geukensia demissa*; 2.09 kJ/g wet weight; McKinney et al. 2004), mummichogs (*Fundulus heteroclitus*; 4.23 kJ/g wet weight; Dunn 1974), or seaweed (*Ulva lactuca*; 1.60 kJ/g wet weight; Shpigel et al. 1999), with all crabs having access to sediment, to isolate the effects of each food type and determine the maximum change in fitness induced by a dietary shift. We collected *G. demissa*, *F. heteroclitus*, and *U. lactuca* from our field site daily to ensure crabs were provided natural fresh food sources. Each of these species is common throughout salt marshes, and all are frequently consumed by blue crabs (Laughlin 1982, Hines 2007, Reichmuth et al. 2009). Because consumers are known to compensate for low-quality diets by increasing the amount of food consumed (Simpson and Simpson 1990, Simpson et al. 1995), we fed crabs either a satiating amount of food (4 ribbed mussels, 25.2 g mummichog, 3.7 g seaweed) or approximately one-quarter this amount (1 ribbed mussel, 5.8 g mummichog, 1.3 g seaweed). The quantities of food offered depended on food type. While mummichog weight corresponded to the average weight of the soft tissue within 4 or 1 mussels, seaweed weight related to the volume of 25.2 or 5.8 g of mummichog because *U. lactuca* is substantially less dense than mummichog and the amount of food blue crabs can consume is dependent on their stomach capacity (Griffen and Mosblack 2011). Thus, this study had a 3x2 factorial design (i.e. food type x portion size) with ten crabs randomly assigned to each of the six different experimental diets. Two weeks after the original 60 crabs were caught, four additional mature female crabs were collected and starved for two months in chambers with sediment to compare the effects of starvation to our food treatments. Starved crabs were excluded from all statistical analyses due to the lower number of replicates and later collection date, but were included in figures as visual references.

Crabs were fed a constant experimental diet every other day, and any excess food was removed after 24 h. Mussels were cracked open prior to being fed to the crabs in an effort to make handling effort more similar across food types, and only soft tissue weights of mussels were used in analyses. A generalized linear model (GLM) with a binomial distribution was employed to determine if either the food type (mussel, fish, or seaweed) or amount of food offered (large or small portions) influenced crab mortality. All statistical analyses were conducted in R, version 3.0.2 (R Development Core Team, Auckland, New Zealand). We originally included experimental block and holding tank as blocking factors in the statistical models described below, however, these were not significant, and so data were pooled across blocks and tanks for all analyses.

Behavior measurements

We assessed individual crab aggression levels daily to determine if diet influenced behavior. To reduce biases in behavior originating from previous feeding history, we did not begin measuring behavior until two weeks after capture. Behavior was measured by slowly lowering a metal prong (25.0 cm x 0.5 cm) into each container, stopping approximately three cm from the mouth of the crab, and observing the crab response. The container sides were opaque to help prevent the crab from reacting to stimuli outside of the container, and the observer was careful to never appear directly over the container. Similar techniques have been used previously to examine the aggressive behavior of animals (e.g. squid; Sinn et al. 2010). Crab behavior was categorized as aggressive if the crab approached or raised its chelipeds towards the prong, while stationary crabs or crabs that moved away from the prong were labeled as docile. Crab behavior was measured once each day between the hours 1200–1330 prior to feeding to help control for any behaviors associated with the crab circadian rhythm and to prevent changes in behavior associated with consuming food. We examined the factors that influenced crab behavior using a mixed–effects GLM with a binomial distribution. The response variable in this analysis was crab behavior on each sampling day (aggressive or docile). We treated food type, portion size offered, time since last fed (24 or 48 h), and daily temperature as fixed factors, and individual crab ID as a random factor to control for repeated measures of each individual crab. For presentation purposes only, data are shown as the proportion of observations where crabs were aggressive for each factor.

Tissue Analysis

At the end of the experiment, crabs were dissected and the primary energy storage organ of crabs, the hepatopancreas (Parvathy 1971), was removed to assess the relative physiological condition of individuals. Similarly, both the ovaries and developing eggs were removed. These were combined with any egg masses the crab produced during the experiment to determine the amount of tissue crabs invested in reproduction. The hepatopancreas, reproductive tissues, and remainder of the crab were dried separately at 70 °C for 72-h. The mass of the hepatopancreas was divided by the dry mass of the rest of the crab to produce a size independent index of longterm energy stores (hepatosomatic index; HSI) following the protocol of (Riley et al. 2014). Likewise, the mass of the reproductive tissue underwent an analogous calculation to produce a size independent index of reproductive effort (gonadosomatic index; GSI). We performed separate 2-way ANOVAs to determine how food type and portion size offered influenced HSI and GSI, followed by Tukey's multiple comparison tests. Prior to this and all subsequent statistical analyses, Shapiro–Wilk tests of normality and homogeneity of variance were conducted.

We also assessed long-term energy storage in terms of hepatopancreas lipids. We determined the bulk lipid content of the hepatopancreas using a modified Folch method where chloroform was replaced with hexanes (Pickova et al. 1997, Undeland et al. 1998).We determined the percent lipid composition of the hepatopancreas by dividing the dry weight of the extracted lipids with the initial hepatopancreas dry weight. In order to clearly present the relationship between hepatopancreas condition and diet, we conducted a 2-way ANOVA to assess the impact of food type and portion size offered on the percent lipid of the hepatopancreas as well as a linear model II regression correlating the HSI of the hepatopancreas to the % lipids of the hepatopancreas.

Crab oocytes were analyzed by rehydrating subsamples of eggs from each crab using filtered seawater and photographed under a dissecting microscope to determine the average egg volume (μm^3). Ten eggs were randomly selected from each crab, and the areas of the eggs were computed using the software SIGMA Photo Pro version 5.5.2. This allowed us to back-calculate the volume of the eggs by applying the equation for a sphere. To roughly estimate the number of eggs produced by each crab, we calculated the average mass of an individual egg using the previously determined egg volumes for each crab and assuming that eggs had the same density as water. The total number of eggs generated was obtained by dividing the overall mass of the eggs with the estimated mass of a single egg. Given the unverified assumptions within these calculations, we only use these estimates to compare the relative number of eggs produced between individuals (since identical assumptions were applied across all individuals). Separate 2-way ANOVAs were used to determine how food type and portion size offered influenced the size and calculated amount of eggs produced. Tukey’s multiple comparison tests were used to determine pairwise differences.

RESULTS

Mortality

In total, six crabs fed seaweed died while only one crab fed mussels died, and there was no mortality in crabs fed a fish diet. Crabs fed seaweed were found to have significantly higher mortality than crabs fed either fish or mussels (GLM, df = 3, t = -2.908, $P = 0.0052$), but the amount of food offered did not significantly alter mortality (GLM, df = 3, t = 0.268, $P = 0.7893$).

Behavior

Both food type and amount of food offered significantly affected crab behavior. Crabs which consumed seaweed were over twice as likely to be aggressive (41% of time) as compared to crabs which consumed animal matter (aggressive19% of time) (mixed–effects GLM; Z = 3.86, $P = 0.0011$), while there was no significant difference in behavior between crabs which consumed either mussels or fish (mixed–effects GLM; Z = 0.51, $P = 0.6096$; Figure 3.1A). Crab aggression levels decreased as food portion size increased (mixed–effects GLM; Z = 4.95, $P < 0.0001$).We found a significant interaction between food type and portion size on behavior (mixed–effects GLM; Z = -4.18, $P < 0.0001$) so that crabs which consumed seaweed exhibited higher aggression when fed more (Figure 3.1A).

Additionally, crab aggression significantly decreased with increasing temperature (mixed–effects GLM; Z = -4.98, $P < 0.0001$; Figure 3.1B). Time since feeding also influenced aggression, with crabs aggressive 24% of the time 24 h after feeding and 45% of the time 48 h after feeding (mixed–effects GLM; Z = 2.07 $P = 0.0383$; Figure 3.1C). Aggressive behavior was also consistent through time for individuals, regardless of experimental conditions as indicated by the significant random effect of individual (Chi-square = 107.25 comparing model with and without random effect, df = 1, $P < 0.0001$).

Tissue analysis: Energy storage

Diet had a strong influence on crab energy stores. The physiological condition of crabs as denoted by HSI was significantly affected by food type and portion size (2-way ANOVA; food type: F = 60.19, df = 2, $P < 0.0001$; portion size: F = 58.31, df = 1, $P < 0.0001$). Crabs fed large portions of animal matter stored on average three times more energy than crabs fed small portions of animal matter, and over 14 times more than crabs fed seaweed (Figure 3.2A). Food type and portion size interacted such that crabs fed seaweed produced the same size energy stores regardless of portion size (2-way ANOVA; F = 20.60, df = 2, $P < 0.0001$; Table 3.1).

Similar patterns were observed in terms of lipid storage, as both food type and amount of food offered interacted to influence the lipid content of the hepatopancreas (2-way ANOVA; df = 2, F = 6.12, $P = 0.0039$; Figure 3.3A). The hepatopancreas lipid content for crabs fed animal matter was over three times higher than for crabs fed seaweed, regardless of portion size (2-way ANOVA; df = 3, F = 24.09, $P < 0.0001$). On average, the lipid content of the hepatopancreas of crabs fed large portions of food was 67% higher than for crabs fed small portions of food (Figure 3.4A). However, only crabs fed mussels had a significant difference in lipid content between portion sizes (2-way ANOVA; df = 1, F = 22.90, $P < 0.0001$) The lipid content of the hepatopancreas and HSI were strongly correlated as lipid content explained 64% of the variation in HSI (linear regression; df = 58, t = 10.16, $P < 0.0001$; Figure 3.3B). In other words, crab hepatopancreases became larger with an increase in their lipid composition.

Tissue analysis: Reproductive potential

Similar to the physiological condition of crabs, the reproductive effort of crabs as indicated by GSI was also significantly affected by both food type and portion size (2-way ANOVA; food type: F = 39.02 df = 2, $P < 0.0001$; portion size: F = 47.89 df = 1, $P < 0.0001$). Crabs fed large portions of animal matter invested on average nearly three times more towards reproduction than crabs fed small portions of animal matter, and almost 10 times the amount invested by crabs fed seaweed (Figure 3.2B). Food type and portion size interacted so crabs that consumed seaweed invested the same amount of tissue towards reproduction regardless of portion size (2-way ANOVA; F = 12.21, df = 2, $P < 0.0001$; see Table 3.1 for pairwise comparisons).

The mean volume of eggs crabs produced also depended upon both food type and portion size (2-way ANOVA; food type: F = 12.41, df = 2, $P < 0.0001$; portion size: F = 6.09, df = 1, $P = 0.0171$). Although there was not a significant difference in egg size between crabs fed the same portions of fish and mussels, crabs fed large portions of animal matter produced eggs 25% larger than crabs given small portions of animal matter, and 55% larger than crabs given seaweed (Figure 3.4; Table 3.1). Food type and portion size were not found to interact (2-way ANOVA; F = 2.105, df = 2, *P* < 0.1325). Likewise, both food type and portion size regulated the relative number of eggs crabs produced (2-way ANOVA; food type: F = 16.41, df = 2, *P* < 0.0002; portion size: F = 8.91, df = 1, *P* = 0.0044). Crabs produced almost three times more eggs when given large portions of animal matter than when given seaweed or small portions of animal matter. Food type and portion size did not interact to influence egg numbers (2-way ANOVA; F = 2.29, df = 2, *P* = 0.1116).

DISCUSSION

By experimentally controlling the diet of the commercially harvested blue crab, *Callinectes sapidus*, we demonstrate that diet has a strong impact on crab mortality, fecundity, physiological condition, and behavior. *C. sapidus* fed seaweed invested significantly less tissue in reproduction and internal energy stores, and exhibited substantially higher mortality and aggression than crabs fed animal matter. Studies on the carnivorous rock crab *Cancer irroratus* (Griffen and Riley 2015), on the omnivorous European green crab *Carcinus maenas* (Griffen 2014), and on the herbivorous mangrove tree crab *Aratus pisonii* (Riley et al. 2014) all report similar findings across the dietary continuum from carnivores to herbivores–that increased consumption of animal tissue improves the fecundity and physiological condition of crabs. These results have important implications for individuals and populations that switch from consuming primarily animal tissue to diets that consist predominantly of algae and plant matter.

Seaweed diets may have reduced crab fitness through several non-mutually exclusive processes. Although blue crabs frequently consume *Ulva lactuca*, seaweed normally constitutes less than 10% of the material blue crabs consume in healthy ecosystems (Dittel et al. 2006, Hines 2007). Exclusive consumption of *U. lactuca* in this experiment could have reduced fitness via the buildup of toxic exudates (Johnson and Welsh 1985) or by providing insufficient nutrition. Seaweed has high levels of indigestible material (~20% cellulose and hemicellulose) as well as relatively low levels of nitrogen and lipids compared to animal tissue (Wolcott and O'Connor 1992, Herbetreau et al. 1997, Linton and Greenaway 2007). Nitrogen limitation in particular is a common phenomenon among herbivorous crabs (Wolcott and O'Connor 1992).

Behavior

Crab aggression levels increased with the consumption of seaweed and decreased with portion size. Seaweed may have increased crab aggression either through hormonal changes or by partially starving the crabs. Leopoldo et al. (2010) report that the amino acid tryptophan can suppress the aggressiveness of mud crabs, whereas Hazlett et al. (1975) and Stocker and Huber (2001) have documented increased aggression in crustaceans under starvation conditions. These two mechanisms may have worked in concert to raise crab aggression since *U. lactuca* has relatively low concentrations of tryptophan compared to animal tissue and other protein sources (Vinoj Kumar and Kaladharan 2007). More research will be necessary to separate the relative influence of starvation and tryptophan on crab behavior; although the increase in crab aggression during each 48-h feeding period coupled with physiological condition implies the primary driving force for the behavior change is starvation.

Tissue analysis

The hepatopancreas is the main energy storage organ of crustaceans, serving as the primary storage site of lipids (long-term energy stores) as well as one of several storage sites of glycogen (short-term energy stores; Parvathy 1971). Depleted hepatopancreas lipid stores are indicative of starvation (Sanchez-Paz et al. 2007), and have been suggested to reduce reproduction (Vazquez Boucard et al. 2004). The consumption of seaweed probably reduced crab energy stores because typically the lipid content of seaweed is less than 4% (Herbetreau et al. 1997) and *U. lactuca* in particular has a lipid content below 0.5% (Ortiz et al. 2006). Similarly, crabs fed small portions of mussels likely exhibited significantly lower lipid stores than crabs fed fish because ribbed mussels contain considerably less lipids (~5%) as a proportion of dry weight than mummichogs (~10%) (Bergen et al. 2001, Weinsteinet al. 2009). Although crabs can build lipid stores through lipid anabolism from excess proteins and carbohydrates, the process is not as efficient as the direct uptake of lipids through lipid rich diets (Kucharski and Da Silva 1991). These differences in the lipid content of the food and corresponding decline in lipid storage of the hepatopancreas are likely responsible for the observed decrease in reproductive effort because the size and amount of eggs produced depends on the availability of lipids (Doughty and Shine 1997). A portion of the GSI as measured here was comprised of extruded eggs, while the remainder was comprised of vitellogenic ovaries. Smaller vitellogenic ovaries should translate directly into lower reproductive output in *C. sapidus*, as the amount of eggs crabs produce is directly proportional to gonad mass (Hartnoll 2006, Griffen 2014). Furthermore, larval mortality in crustaceans and fish is negatively correlated to egg size (Bagenal 1969, Gimenez and Anger 2001, Gimenez and Anger 2003). This implies that crabs which consume seaweed should yield larvae with higher mortality than crabs which consume animal matter because crabs fed seaweed generally produced eggs 30% smaller than crabs fed animal matter. Crabs may have compensated for increasing the size of their eggs by decreasing the amount of eggs generated. However, a rough calculation of the number of eggs each crab produced determined that brood size increased with the amount and type of food consumed. In fact, calculated egg size and egg number were positively correlated, meaning that crabs simultaneously increased both egg quality and number when their diet improved, consistent with patterns in other crab species (Riley et al. 2014). Such a pattern was likely observed because the improved diet provided more energy and nutrients for crabs to invest towards reproduction.

Fishery implications

These findings have implications for blue crab fisheries, as the experimental diet shifts imposed here (algal consumption and lower consumption overall) are similar to diets documented by Reichmuth et al. (2009) for crabs in estuaries that are heavily contaminated by heavy metals. The increased mortality coupled with the decreased reproductive potential and energy reserves of crabs consuming seaweed substantially reduced their fitness in comparison to crabs consuming animal tissue. Thus, the dietary shift documented by Reichmuth et al. (2009) potentially causes the *C. sapidus* population of metal polluted estuaries to experience lower population growth than populations within clean estuaries. Indeed, our study presents a conservative estimate of the impacts of metal pollution because we only examined the implications of diet shift alone, and these are probably further exacerbated when the toxic effects of the pollutant that caused the diet shift are taken into account. It should be recognized that our results depict the maximum change in fitness induced by a dietary shift, since we examined the effects of pure animal and pure plant diets. By contrast, crabs experiencing metal pollution shift their diets towards greater herbivory, but still ingest some animal matter (Reichmuth et al. 2009). Our results suggest that decreasing the amount of animal matter consumed, without entirely eliminating it, can still have a substantial impact on fitness. Diet mixing can be an effective strategy and is known to increase fitness relative to single diets (Coll and Guershon 2002). However, previous work across a range of crab species indicates that mixing plant and animal foods in the diet does not offer any benefit for fecundity or energy storage relative to carnivorous diets alone (Griffen 2014, Riley et al. 2014, Griffen and Norelli 2015, Griffen and Riley 2015). Diet mixing or shifting from animal tissue to predominantly seaweed diets by crabs within polluted estuaries may alternatively benefit crabs by helping reduce the amount of metals crabs accumulate, since toxins can biomagnify up trophic levels (Guthrie et al. 1979). However, most marine invertebrates primarily accumulate toxins by uptake from the surrounding water column (Gray 2002). Many other types of pollutants besides metals, ranging from pesticides to polycyclic aromatic hydrocarbons (PAHs; fossil fuel derivatives), are known to impair the foraging behavior of crabs and fish (Little et al. 1990, Weis et al. 2001, Dissanayake et al. 2010), and may indirectly reduce the fitness of exposed species through such dietary changes.

Broader implications for ecology

The research presented here has at least two broader implications for population ecology. First, this study underscores the importance of examining the nonlethal effects of environmental stressors that cause diet shifts. For instance, our results demonstrate that the reproductive effort and physiological condition of crabs may decrease substantially from the indirect effects of pollutants, independent of any direct effects from the pollutants. While many studies document physiological and behavioral changes in response to contaminants (Fleeger et al. 2003, Macneale et al. 2010), relatively few studies have explored how these indirect effects may alter the fitness of organisms (but see (Relyea and Diecks 2008, Duquesne and Leiss 2010, Hanlon and Relyea 2013). The tight link between diet and fitness also reveals the necessity of including dietary shifts when predicting population responses to environmental change. Many current environmental issues such as climate change (Montevecchi and Myers 1997, Kitaysky 2006) and species invasions (Eagles-Smith 2008) are accompanied with drastic changes in diet. However, when calculating the community and population response to these changes, the indirect effect of dietary shifts are frequently either ignored or considered too complex to incorporate (McBride et al. 2014). Our results imply that, when indirect effects from diet shifts are included, these environmental changes may have larger effects than previously anticipated.

Second, the positive correlation between the number of eggs produced and their size shows that individuals may improve offspring quantity and quality simultaneously. The well-known r- and K-selection theory postulates that species try to maximize fitness by producing either a large amount of low quality offspring or a small amount of high quality offspring depending on their life history strategy (McBride et al. 2014). As energy stores are finite, species must trade-off between quantity and quality (Pianka 1970, Smith CC, Fretwell 1970). In contrast, our findings suggest that during times of abundant resources some organisms will bet–hedge by simultaneously employing both options: increasing egg quantity and enhancing egg quality.

In conclusion, fecundity, physiological condition, and behavior are significantly influenced by diet. Our experiments show that the fitness of an important fishery species was enhanced with increased consumption of animal tissue while the consumption of seaweed reduced the fecundity and long-term energy stores as well as increased the mortality and aggression of *C. sapidus*. This study reveals the impacts that diet selection can have on individuals' performance and on the potential for population growth of this important fishery species.

ACKNOWLEDGEMENTS

Thanks to Melody Jackson and Alex Norelli for assistance in capturing and feeding the crabs as well as the Baruch Institute for access to their facilities. Funding was provided by National Science Foundation grant no. OCE-1129166, the University of South Carolina, and the Ohio Mayflower Society.

Table 3.1 Analysis of Tukey's HSD multiple comparison test to determine pairwise differences in the gonadosomatic index (GSI), hepatosomatic index (HSI), egg volume, and egg number of crabs given different diets.

Comparison	**GSI** **_p_-value**	**HSI** **_p_-value**	**Egg Volume** **_p_-value**	**Egg Number** **_p_-value**
Mussel Large–Fish Large	0.9996	0.9764	0.4247	0.8976
Seaweed Large–Fish Large	< *0.0001*	< *0.0001*	*0.0001*	*0.0023*
Fish Small–Fish Large	< *0.0001*	< *0.0001*	0.1034	0.4299
Mussel Small–Fish Large	< *0.0001*	< *0.0001*	*0.0109*	0.3108
Seaweed Small–Fish Large	< *0.0001*	< *0.0001*	*0.0003*	*0.0014*
Seaweed Large–Mussel Large	< *0.0001*	< *0.0001*	*0.0302*	<*0.0001*
Fish Small–Mussel Large	< *0.0001*	< *0.0001*	0.9675	*0.0452*
Mussel Small–Mussel Large	< *0.0001*	< *0.0001*	0.4770	*0.0308*
Seaweed Small–Mussel Large	< *0.0001*	< *0.0001*	*0.0467*	<*0.0001*
Fish Small–Seaweed Large	0.0578	*0.0015*	0.1873	0.2152
Mussel Small–Seaweed Large	0.4145	*0.0472*	0.8428	0.4407
Seaweed Small–Seaweed Large	1.000	0.9615	0.9999	0.9999
Mussel Small–Fish Small	0.9167	0.8448	0.8985	0.9995
Seaweed Small–Fish Small	0.0533	*0.0185*	0.2840	0.1612
Seaweed Small–Mussel Small	0.3951	0.2772	0.9160	0.3589

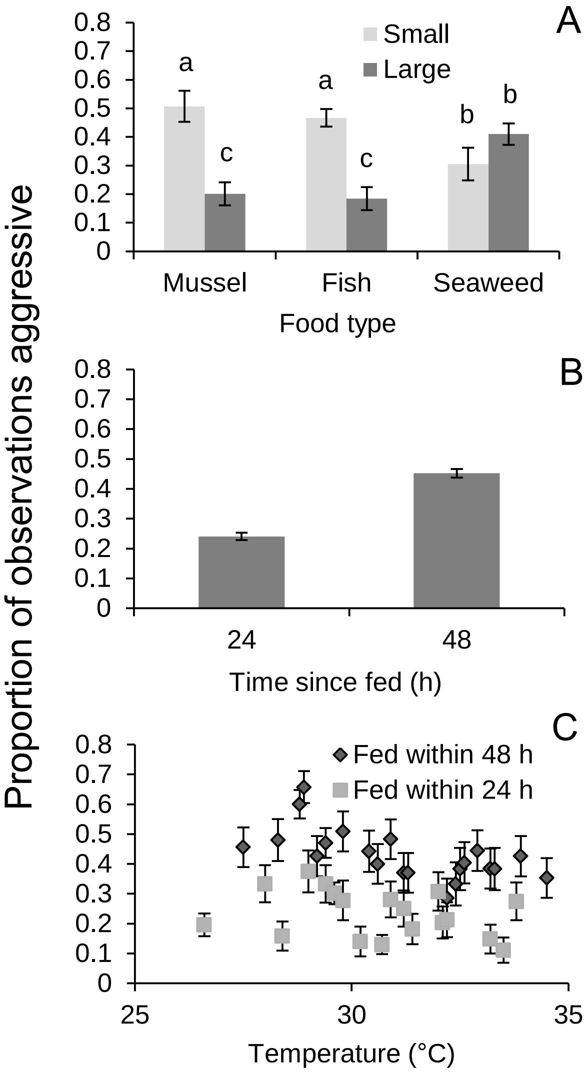

Figure 3.1 Analysis of crab behavior. Mean ± SE aggression probability of crabs as a function of **(A)** diet (n = 10), **(B)** time since last feeding (24 or 48 h; n = 1168 and 1163 respectively), and **(C)** daily temperature (°C) within holding containers for crabs fed within 24 or 48 h (n = 53–159). Replicates depend on the number of surviving crabs and times exposed to the same temperature (max = 3 same temperature).

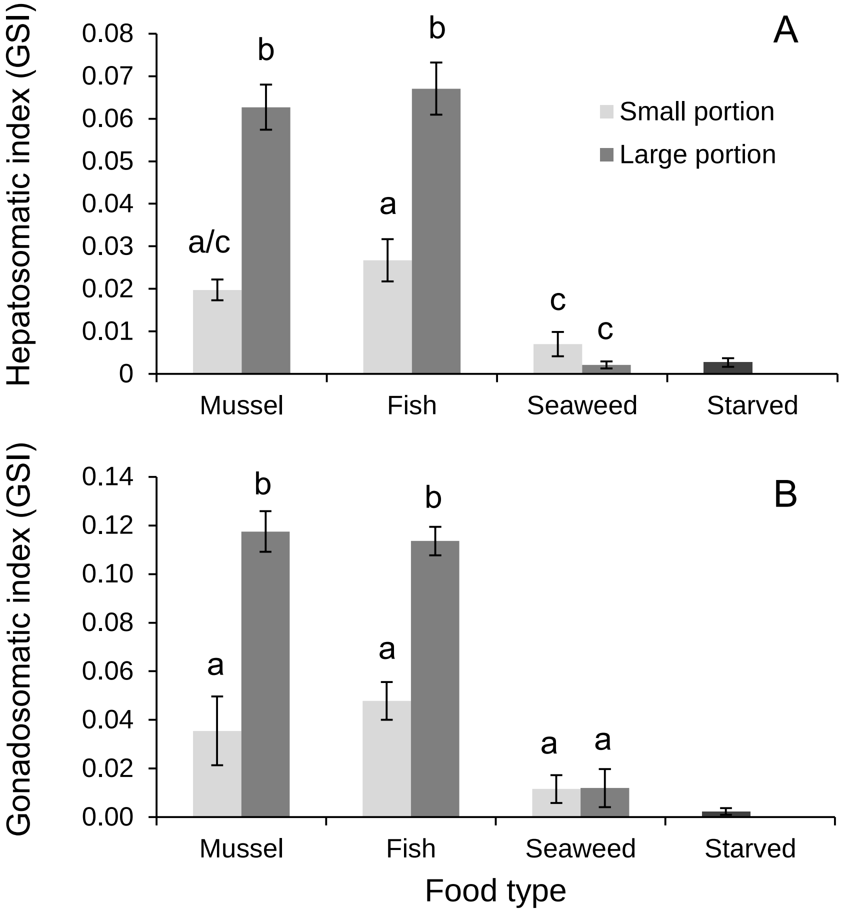

Figure 3.2 Effect of diet on tissue investment towards the hepatopancreas and reproduction. Mean ± SE **(A)** hepatosomatic index (HSI) and **(B)** gonadosomatic index (GSI) of crabs fed either ribbed mussels (*Geukensia demissa*), fish (*Fundulus heteroclitus*), or seaweed (*Ulva lactuca*) at one of two portion sizes (large or small) for ~2.5 months (n = 10). For reference purposes, starved crabs were expressed in the figures as separate columns (n = 4). Starved crabs were not used in the statistical analyses.

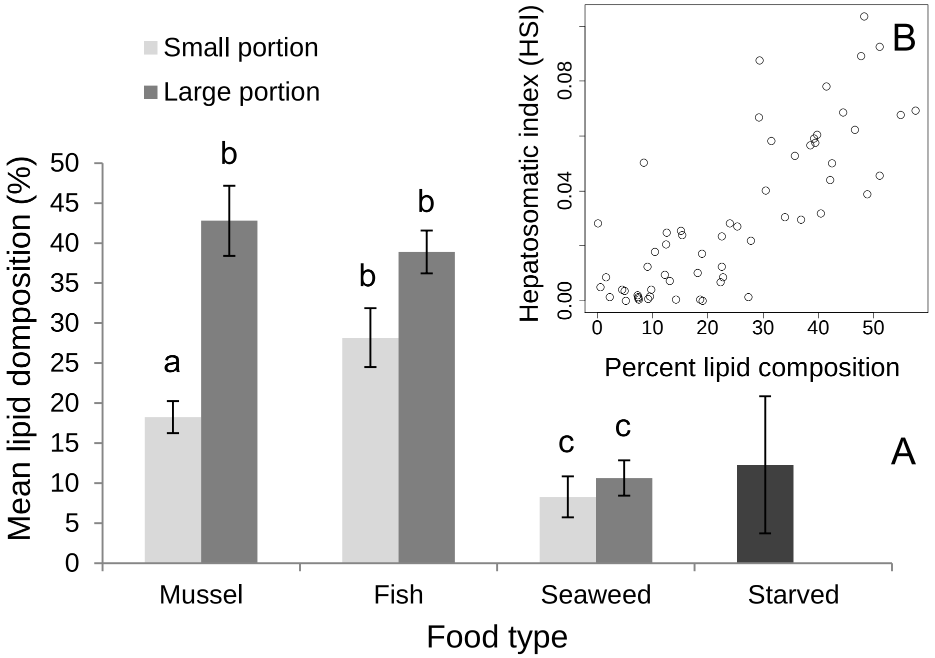

Figure 3.3 (A) Analysis of percent lipid composition of the hepatopancreas. The effect of food type (ribbed mussels, *Geukensia demissa*; mummichogs, *Fundulus heteroclitus*; seaweed, *Ulva lactuca*) and portion size offered (large, small) on the mean ± SE percent lipid composition of the crab hepatopancreas ($n = 10$). Starved crabs ($n = 4$) were represented in the figure to serve as a visual reference and were not included in the statistical analysis. Lower case letters denote statistical differences ($p < 0.001$, 2-way ANOVA, Tukey test). **(B)** The relationship of percent lipid composition of the hepatopancreas for individual crabs and their corresponding hepatosomatic index (HSI, $n = 60$).

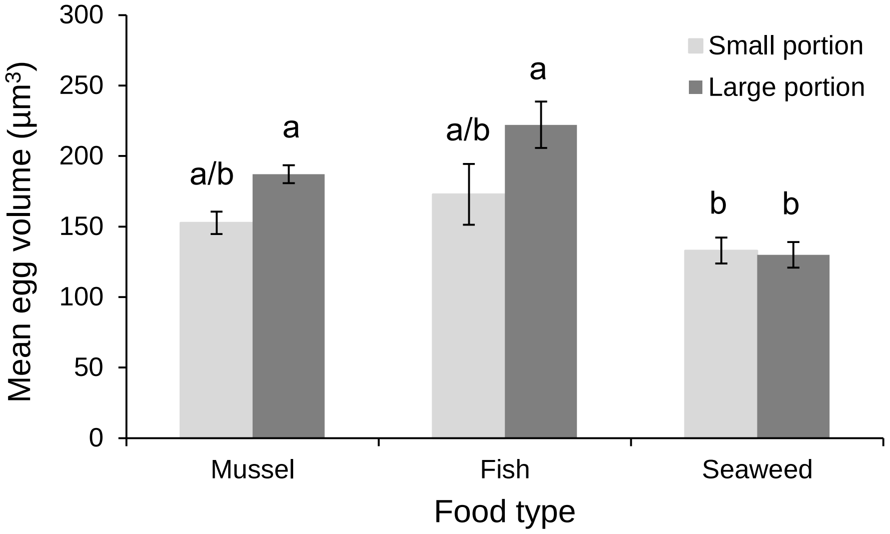

Figure 3.4 Effect of diet on egg size. Mean ± SE egg volume (μm^3) of crabs fed either ribbed mussels (*Geukensia demissa*), fish (*Fundulus heteroclitus*), or seaweed (*Ulva lactuca*) at one of two portion sizes (large or small) for ~2.5 months (n = 10).

CHAPTER 4

INDIVIDUAL PERSONALITY ASSOCIATED WITH INTERACTIONS BETWEEN PHYSIOLOGICAL CONDITION AND THE ENVIRONMENT[3]

ABSTRACT

An emerging focus of behavioral ecology is to determine the driving forces behind animal personalities. While numerous theories have been proposed to explain these behavioral variations, empirical studies on this subject remain lacking. Here, we test ecological theory by studying the combined effects of physiological condition and habitat quality on the behavior of individual mud crabs, *Panopeus herbstii*, across the spawning season (early spawning season and 2 months after). We assessed the boldness, energy stores and reproductive effort of crabs collected across 10 oyster reefs of low and high quality using laboratory observations and subsequent dissections. Crab boldness was significantly dependent on the interaction between habitat quality and season. While crab behavior remained relatively constant on healthy reefs, crabs on degraded reefs exhibited a nearly two-fold increase in boldness during the late spawning season, approximating the boldness of crabs on healthy reefs. This behavioral change corresponds to a seasonal shift in crab energy store content and is likely to represent a switch in the primary driving force of crab behavior. During the early season, crab boldness was positively correlated with short-term stores, whereas later in the season, crab boldness was negatively

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[3] Belgrad, B.A., J. Karan, and B.D. Griffen. *Animal Behaviour*. 123: 277-284. Reprinted here with permission of publisher.

correlated with long-term stores. Our results suggest that behavior is driven by predation pressure and refuge availability during the early spawning season, but afterwards depends on replenishing energy stores used for reproduction. These findings support ecological theory and also provide new insight into the stability of behavioral drivers.

INTRODUCTION

Consistent individual differences in animal behavior (i.e. animal personalities) have increasingly been recognized as an important ecological and evolutionary attribute of wild populations (Pennisi 2016). Animal personalities have been associated with differences in mortality (Stamps 2007), offspring production (Both et al 2005) and interspecific interactions (Chapter 6), which can scale to have an impact on the persistence of populations (Pruitt and Goodnight 2014). At the community level, these behavioral variations can influence the spread of diseases (Barber and Dingemanse 2010, Krause et al. 2010), regulate trophic cascades (Ioannou et al. 2008, Griffen et al. 2012) and have even been implicated as a mechanism to facilitate speciation (Wolf and Weissing 2012) and invasion success (Chapple et al. 2012, Carere and Gherardi 2013). Understanding the factors that govern personalities has therefore become a fundamental goal of behavioral ecologists and physiologists.

Recent attempts to explain the emergence of personalities have emphasized the importance of state–behavior feedbacks (Biro and Stamps 2008, Dingemanse and Wolf 2010, Wolf and Weissing 2010, Sih et al. 2015). Under this framework, behavioral variations arise as a result of differences in individual state (e.g. individuals of larger size are bolder and better able to find food, thereby increasing their size and reinforcing their tendency to be bold; Luttbeg and Sih 2010). Here, the concept of state refers not only to organismal attributes such as individual size or physiological condition, but also includes external attributes such as habitat quality or season. Several studies have previously determined that behavioral variations can correlate with such individual–level characteristics as metabolism (Careau et al. 2008, Toscano and Monaco 2015) and hunger level (Stocker and Huber 2001, Chapter 3). Additionally, the environmental parameters of temperature (Biro et al. 2010), predator presence (Briffa et al. 2008), food availability (Kontiainen et al. 2009) and time of day (Dingemanse et al. 2002) have also been found to influence the personality of individuals. However, empirical studies that evaluate the relationship between individual state and personality remain limited, and none to our knowledge examine the interaction between individual–level and environmental variables on personality simultaneously.

In the present study, we investigate how personality is linked to physiological condition and habitat quality. Ecological theory postulates that short–term behavioral consistency can be achieved through asset protection and starvation avoidance. Individuals that have high assets (i.e. are in good physiological condition with high energy stores or egg masses) should be shy and unaggressive to safeguard those assets, whereas those individuals who lack assets should be bold and aggressive to obtain more assets (McElreath et al. 2007, Wolf et al. 2007). Similarly, animals close to starvation must be bold to find food and avoid starving to death, whereas individuals not close to starvation may be cautious to avoid unnecessary risks such as increased predation (Houston and McNamara 1999). Theory also predicts that differences in personality can be driven by severe differences in the quality of habitat experienced by different members of a population. When members of a population are in high-quality habitats, individuals are expected to be bold because of an abundance of resources and low risk. In contrast, individuals are expected to become shy in low-quality habitats that have few resources and high risk to elude predators, with only hungry individuals becoming briefly bold to avoid starving (Luttbeg and Sih 2010). Here, we study how these physiological and environmental feedbacks may interact to have an impact on personality across the spawning season. We do this by examining personality and physiological condition of individuals collected from high– and low–quality habitats. We chose a study system with extensive spatial variation in habitat quality, but where organism movement was restricted to specific regions over the short term (weeks to months) owing to the patchiness of the habitat, to test the above ecological theories.

METHODS

Study system

We studied the interactive effects between physiological condition and habitat quality on personality using a commercially and ecology important coastal community. Oyster reefs serve as a valuable environment for a variety of fishes and invertebrates by providing structural complexity and a hard surface on an otherwise flat, soft–sediment seafloor (Wells 1961, Tolley and Volety 2005). Over the past 130 years, oyster reefs have become one of the most degraded habitats worldwide as 85% of the reefs have been lost (Beck et al. 2009) as a result of harvesting, sedimentation, hypoxia, disease and introduced species (Ford and Tripp 1996, Lenihan and Peterson 1998). Reef degradation usually results in a loss of architectural complexity and food sources, which can have cascading effects that have a negative impact on a number of species (Lenihan et al., 2001, Griffen and Norelli 2015). Thus, whereas healthy oyster reefs have an abundance of food resources and ample interstitial spaces for refuge, degraded reefs have both low food and poor refuge.

The mud crab, *Panopeus herbstii*, is a common inhabitant of oyster reefs along the southeast and Gulf coasts of North America. Here, the crab predominantly consumes small bivalves such as the scorched mussel, *Brachidontes exustus*, but may also consume barnacles, algae and detritus (Griffen and Mosblack 2011). Mud crabs remain rather stationary compared with other species, as both male and female individuals often stay on the same reef for months (Toscano et al. 2014b), but may move >5 m over 2 days (Stachowicz and Hay 1999). Crab movement on reefs is primarily attributed to foraging (Stachowicz and Hay 1999), but can also include brief competitive interactions and mate searching (B.A. Belgrad, personal observations). Individuals greatly reduce their activity levels and increase their time in refuge in the presence of predators (Hughes et al. 2014), and exhibit a bold–shy continuum of personality types (Griffen et al. 2012, Toscano et al. 2014). Female crabs generally mature by the time they reach a carapace width of 16 mm (Hines 1989). The peak spawning season typically occurs during May, but vitellogenic and gravid crabs can be found from March to October, with crabs normally producing a single brood throughout the year (McDonald 1982).

Collection

We sampled five healthy reefs and five degraded reefs within North Inlet National Estuarine Research Reserve (33°20’N, 79°10’W, Georgetown, SC, U.S.A.) to assess the effect of reef quality on mud crab behavior and physiological condition. Reef height was used as a proxy for reef quality, as the growth and survival of oysters as well as the number of mussel prey increases with reef height (Griffen and Norelli 2015, Lenihan and

Peterson 1998). Reefs with heights less than 12 cm were considered degraded, whereas those with heights greater than 20 cm were considered flourishing, healthy reefs. We calculated reef height using the average of 10 measurements taken at random locations within each reef, each one measuring the height from the tip of oyster shells to the substrate surface (Griffen and Norelli 2015). Reefs were chosen in close proximity to each other to reduce confounding environmental variables brought about by large spatial scales, but far enough apart to ensure that crabs could not travel between sampled reefs (mean ± SD distance between nearest–neighbor reefs = 245.4 ± 631.5 m; Stachowicz and Hay 1999, Toscano et al. 2014b). The quality of the reefs sampled was randomized over the collection period so there was no trend between sampling day and reef height (linear model: t = 0.95, $P = 0.35$).

Within each reef, we collected 10 mature female mud crabs, *P. herbstii*, between 17 and 27 mm in carapace width to diminish differences in behavior associated with size (carapace width ± SD for all crabs = 22.7 ± 2.3 mm). Only female crabs were collected because we were interested in the relationship between individual behavior and several physiological parameters. As many of these parameters (e.g. reproductive investment) are known to substantially vary across gender, males were excluded from the study. Sampling was conducted at low tide during the early spawning season (2 weeks in mid–May 2015), and again 2 months after this period (2 weeks in early August 2015; McDonald 1982) to assess seasonal differences in behavior and physiology. During the peak spawning season, we collected both gravid (N = 6) and nongravid (N = 94) crabs, while during the second sampling period only nongravid (N = 100) crabs were collected.

Crabs collected from North Inlet were brought to the Baruch Institute wet laboratory for behavioral analysis and dissection.

Behavioral analysis

We performed behavioral observations to determine the effect of reef quality on crab boldness (i.e. refuge use). Previous work in our laboratory has determined that differences in refuge use between individuals can persist over months (Toscano et al. 2014b), are consistent across multiple conditions (e.g. predator present/absent; Griffen et al. 2012) and are correlated with individual metabolic strategies (Toscano and Monaco 2015). Crabs were blocked through time by reef identity, producing 10 blocks over each sampling period. Boldness was measured following the behavioral assay protocol used in Griffen et al. (2012) and Toscano et al. (2014b). Crabs from both high-quality and low-quality reefs were exposed to a common garden experiment where individuals were exposed to artificial reefs of intermediate integrity with predator and prey odour cues as well as ample structure to provide refuge. All crabs were deprived of food for 24 h prior to observing their behavior to standardize their hunger levels. Each crab was observed in a separate plastic mesocosm (40 x 22 cm and 20 cm high) containing approximately 2 cm of sediment under an approximately 8 cm matrix of cleaned oyster shells covering the entire tank bottom. We used flow–through mesocosms, supplied with seawater from North Inlet. Before entering the mesocosms, sea water was first pumped through a head tank, which contained a single mature oyster toadfish, *Opsanus tau*, to ensure kairomones were distributed throughout the water. Each mesocosm contained eight scorched mussels, *B. exustus*, suspended near the water surface in a mesh bag out of reach of crabs to release prey chemical cues and induce crab foraging behavior.

Crabs were observed at night generally from 2000 to 2300 hours under red light and with the observer behind blinds to minimize crab disturbance. We allowed crabs to acclimate for 10 min in the mesocosms, after which their boldness was observed once every 6 min over 3 h (30 observations for each crab). Boldness was measured as the proportion of the 30 observations in which crabs were not hidden underneath oyster shells. When crabs were outside of refuge, they were frequently seen moving across the shells or foraging (i.e. were active), although on some occasions, nonsheltered crabs were completely still. Following these observations, crabs were placed in a freezer (–20 °C) for later dissection. To broadly examine the combined influence of the environmental parameters habitat and season on individual crab behavior, we analyzed the data using a mixed–effects generalized linear model (GLM; R package: lme4). Because crab boldness (the response variable) was proportional, we modelled this behavior with a binomial distribution (Bolker et al. 2009). Reef quality and collection period were treated as fixed effects with an interaction term while reef and crab identities were treated as random effects to control for nonindependence of crabs within the same block and for repeated measures of each individual crab. Tukey's multiple comparison test was used to determine pairwise differences in behavior (R package: *lsmeans*). This and all other analyses were conducted using R v3.0.3 (R Development Core Team, 2015).

Physiological condition

Crabs were dissected to determine the relationship between physiological condition and individual behavior. To determine the relative physiological condition of crabs, we removed the main energy storage organ, the hepatopancreas (O'Connor and Gilbert 1968, Parvathy 1971). Likewise, we removed the ovaries and any extruded egg clutches from the crab body to assess the reproductive investment of individual crabs. We also removed 50 mg of muscle tissue from the base of the crab pereopods and froze it for later analysis. The hepatopancreas, ovaries, egg masses and crab body remains were each dried separately for 72 h at 70 °C, then weighed to the nearest 0.01 mg. We collected and desiccated 50 mg of muscle tissue from an additional 10 crabs to determine the loss in dry weight of crab remains by the removal of muscle tissue. This additional weight (mean ± SD = 14.95 ± 3.83 mg) was added to the dry weight of crab remains to correct for the earlier removal of muscle tissue. Dry weight of the hepatopancreas as a proportion of crab body dry weight was used as a mass-specific measurement of investment in long–term energy stores (i.e. hepatosomatic index, HSI; Kyomo 1988). Similarly, the dry weight of the reproductive tissues (ovaries + eggs) as a proportion of the crab body dry weight was used as a mass-specific measurement of investment towards reproduction (i.e. gonadosomatic index, GSI; Kyomo 1988). To determine the relative short-term energy stores between individual crabs, we measured the glycogen concentration of the removed muscle tissue (Parvathy 1971). Glycogen content was quantified using a Glycogen Assay Kit MAK016 (Sigma-Aldrich, St Louis, MO, U.S.A.) according to the manufacture protocol. Briefly, 10 mg of the frozen muscle tissue from each crab was homogenized and exposed to a coupled enzyme assay from the kit. This resulted in a colorimetric product (570 nm) proportional to the original glycogen concentration (mg/mg muscle tissue; standardization curve, absorbance = 0.1182 x glycogen concentration, $R^2 = 0.97$). Physiological parameters often vary with size, so we used HSI and GSI as size–independent metrics. Additionally, a mixed–effects GLM determined that there was no significant relationship between individual size and glycogen concentration ($R^2 = 0.05$, estimate = –6.00, t = 1.37, *P* = 0.17).

We examined the effect of physiological condition, spawningseason and habitat quality on crab behavior (proportion of time outside refuge) by running a mixed–effects GLM with a binomial distribution. HSI, GSI, glycogen concentration, carapace width, spawning season and habitat quality were treated as independent fixed effects while crab and reef IDs served as random effects. Spawning season and habitat quality were treated as categorical variables while all others were continuous. Tests for collinearity among the fixed effects without interactions determined that variance inflation factors were low (maximum 1.65). All interactions were initially included in the model and nonsignificant interactions were removed stepwise, from the most complex interaction terms to the simplest, following the protocol of Crawley (2013, pp. 557e578) to help resolve the significance of main effects and achieve the lowest Akaike information criterion (AIC) value. We also conducted three separate generalized linear models using quasi–likelihood with log link functions to determine the effect of reef quality and sampling period on the HSI, muscle glycogen content and carapace width of crabs. Employing quasi–likelihood analysis utilizes the relationship between the mean and variance of the response variable to fit linear models, and is a robust alternative to assigning error distributions to data (Crawley, 2013, pp. 557e578). The GSI of crabs was assessed in a similar way in a fourth test except with the addition of the fixed effect, HSI. Finally, we evaluated the relationship between crab short-term and long-term energy stores using a quasi–likelihood GLM with glycogen content as the response variable and HSI as the explanatory variable.

RESULTS

Behavioral analysis

Crab boldness was substantially influenced by reef quality so that crabs from high–quality reefs increased the amount of time spent exposed relative to crabs from low–quality reefs (estimate = 0.90, Z = 3.01, $P = 0.0026$). These behavior differences across reef quality were magnified early in the spawning season, as sampling period interacted with reef quality to affect behavior (estimate = –0.85, Z = – 5.29, $P < 0.0001$). While crab behavior in high–quality reefs did not change over the spawning season (estimate = 0.11, Z = 1.28, $P = 0.2014$), crab boldness was nearly two–fold lower in low–quality reefs during the first sampling period (estimate = –0.73, Z = –7.27, $P < 0.0001$; Figure 4.1).

Behaviour was also correlated with crab long-term (HSI; estimate = –16.96, Z = –3.65, $P = 0.0003$) and short–term (glycogen content; estimate ¼ 1.70, z ¼ 6.33, P < 0.0001) energy stores. The effect of these energy stores on crab boldness was seasonally dependent. During the early spawning season, crab boldness correlated best with glycogen content, whereas later in the spawning season, boldness negatively correlated with HSI (see insets in Figures 4.2, 4.3). This produced a two-way interactive effect on behavior between HSI and sampling period (estimate = 34.34, Z = 3.65, $P = 0.0003$) as well as a three–way interactive effect between HSI, glycogen content and sampling period (estimate = –115.2359, Z = –12.40, $P < 0.0001$). Finally, the boldness of crabs was dependent on individual size, as larger crabs generally acted bolder than smaller crabs (estimate = 4.61, Z = 4.61, $P < 0.0001$; see insets in Figure 4.4). This produced a three–way interactive effect on behavior between size, reef quality and season (Z = –2.37, *P* = 0.0180), as crabs on high-quality reefs were on average 0.7 ± 2.3 mm (carapace width) larger, and crabs were on average 2 ± 1.7 mm larger in the second sampling period than in the first (Figure 4.4).

Physiological condition

Both HSI and muscle glycogen concentration differed across the spawning season (estimate = –0.39, t = –3.63, *P* < 0.0004; estimate = 0.78, t = 5.24, *P* < 0.0001, respectively), but in opposite directions. Whereas the amount of tissue crabs invested in long–term energy stores dropped on average by 37% after the peak spawning season (Figure 4.2), the muscle glycogen content of crabs almost doubled during the same time frame (Figure 4.3). The amount of tissue crabs invested towards reproduction (i.e. GSI) was also affected by spawning season (estimate = –0.62, t = –2.85, *P* = 0.0049) and reef quality (estimate = –0.36, t = –2.05, *P* = 0.0420). These two factors interacted so that crabs in high–quality reefs invested 80% more tissue towards reproduction later in the spawning season, whereas crabs in low–quality reefs decreased their investment by 14% over this time period (estimate = –34.36, t = –2.79, *P* = 0.0053; Figure 4.5). Unsurprisingly, vitellogenic crabs had the highest GSI, with strong seasonal connections between GSI and HSI (GSI as a function of HSI; estimate = 22.29, t = 2.30, *P* = 0.0216; Figure 4.6). Additionally, the carapace width of crabs significantly increased with habitat quality (estimate = 0.03, t = 2.63, *P* = 0.0092) and spawning season (estimate = 0.09, t = 6.88, *P* < 0.0001; Figure 4.4). Neither long–term nor short–term energy stores were influenced by reef quality (estimate = –0.13, t = –0.96, *P* = 0.3367; estimate = –0.08, t –0.99, *P* = 0.3214, respectively). However, short–term energy stores were inversely related to long–term stores, although this relationship had considerable variation (R^2 = 0.10, estimate = –11.66, t = –3.85, *P* = 0.0002).

DISCUSSION

Our results show that seasonal differences can interact with habitat quality to influence individual fitness with correlations between behavior, energy store utilization and reproductive investment. Crab dissections suggest that behavior initially relates to short–term energy stores (i.e. muscle glycogen content) as well as habitat quality during the early spawning season and on long–term energy stores (i.e. HSI) later in the season. Additionally, reproductive effort substantially varied with habitat quality, but in opposite respects across season. These findings support conceptual theories on state–behaviour feedbacks (Biro and Stamps 2008; Dingemanse and Wolf 2010, Luttbeg and Sih 2010, Wolf and Weissing 2010, Sih et al. 2015), as follows.

The seasonal and spatial variability in mud crab boldness is consistent with the result of two common competing driving forces: predation risk and energetic demands. Crabs on structurally simple, low–quality reefs have significantly higher mortality than crabs on complex, high–quality reefs (Grabowski 2004), and an increase in refuge use has been shown to lower predation risk in this system (Chapter 6). Consequently, mud crabs on low–quality reefs probably were shyer during the typical peak spawning season than crabs on high-quality reefs to compensate for the reduced availability of refuges and to decrease their predation risk at a time when they were producing eggs. After the peak spawning season, mud crabs on low–quality reefs are likely to become bolder to replenish their depleted long–term energy stores, as the energy used for reproduction is generally extracted from energy accumulated in the hepatopancreas (Kyomo1988), which is consistent with the negative correlation between these two indices shown in Figure 4.6. Indeed, mud crab boldness increased when their long–term energy stores were at their lowest (i.e. late spawning season), and was inversely correlated to these stores during this period (insets in Figure 4.2). Differences in boldness between crabs on high– and low–quality reefs may not only affect predation rates, as previously shown (Chapter 6), but may also influence the accumulation rate of energy stores, as an increase in refuge use typically involves a decrease in crab foraging (Grabowski and Kimbro 2005; Griffen et al. 2012). Such results support conceptual predictions that individuals with high assets tend to reduce their risk by becoming shy while those with low assets become bolder to increase their lower reserves (Luttbeg and Sih 2010, Sih et al. 2015). The behavioral patterns observed here can probably be applied to numerous other systems, as predators and energetic demands are ubiquitous forces (Dingemanse and Réale 2005, Quinn and Cresswell 2005, Bell and Sih 2007, Careau et al. 2008, Careau and Garland 2012).

Although the significant three-way interaction between reef quality, season and size prevents us from conclusively determining which factor is primarily responsible for behavior changes, our findings suggest that all three variables play strong roles. Studies in this system (Toscano et al. 2014b; present study) and across numerous phyla (Wilson et al. 1994, López et al. 2005, Brown et al. 2007, Stamps 2007, Biro and Stamps 2008, Sinn et al. 2008) have correlated boldness to increases in individual size. As crabs in healthy reefs are larger and grow more throughout the season than crabs in low–quality reefs (insets in Figure 4.4), this interaction probably arises because of the common relationship between size and behavior. However, reef quality may also influence crab boldness by providing different levels of predation risk (Lima and Dill 1990) or resources

(Heldt 2013), whereas seasonal changes in temperature (Huey and Pianka 1977), food availability (Stickney 1991) or predation risk (Heithaus and Dill 2002) could also be additional sources of behavioral variation.

Coincident with the seasonal change in behavior, the energy stores of crabs varied substantially with sampling period. The reduction of crab long–term energy stores may have been a consequence of the energetic demands of reproduction (Kyomo 1988), but could also have been a result of crab molting, as hepatopancreas lipid and glycogen reserves usually coincide with molting stage (Parvathy 1971, Tian et al. 2012). This second possibility is more likely for crabs in high–quality reefs than crabs in low-quality reefs, as the reproductive effort of crabs in high–quality reefs increased dramatically over this time frame and remained relatively constant for crabs in low–quality reefs. Additionally, crabs in high–quality reefs have greater food availability and grow larger than crabs in low-quality reefs (Griffen and Norelli 2015; see insets in Figure 4.4), which implies that crabs in high–quality reefs molt more than those in degraded reefs. Crab short–term energy stores (i.e. muscle glycogen concentration) exhibited the opposite pattern of long-term energy stores over season. This may be a result of crabs ceasing to develop their long–term energy stores to fuel reproduction in favor of producing short–term stores for increased activity. Surprisingly, crab energy stores did not vary with reef quality. Crabs may be avoiding dramatic differences in energy stores between reefs by distributing themselves according to the availability of resources (i.e. ideal free distribution of organisms; Fretwell and Lucas, 1969). Crab densities on degraded reefs should therefore be severely reduced compared to those on healthy reefs under these circumstances. Indeed, sampling of crab densities across reef quality has found healthy reefs to sustain densities up to eight–fold higher than degraded reefs (Griffen and Norelli 2015).

The differences in reproductive effort of crabs across habitat integrity coincide with findings by Griffen and Norelli (2015) that degraded reefs support lower egg production than healthy, complex reefs. However, the seasonal variation in reproductive effort suggests that the timing of peak spawning depends on reef quality. Crabs in healthy, food-rich reefs may have delayed spawning to increase their growth. A large investment towards growth early on in the spawning season could explain part of the variation in reproductive effort across reefs as crab egg production increases with body size (Hines 1982). Alternatively, the apparent delay in spawning of crabs on healthy reefs may actually represent a second clutch of eggs. While this species of crab has not been documented to produce multiple egg clutches per season, many other brachyuran crabs at this latitude, including other species of Xanthid crab, commonly produce several broods each year (Darnell et al. 2009, Hines 1982, Hines 1986). The abundance of food/refuge on healthy reefs probably provides enough resources to sustain multiple broods, and previous sampling efforts may have simply missed the first period of egg production if this affluence allows crabs on healthy reefs to rapidly accumulate energy stores and spawn early. Although the full impact of habitat quality on spawning remains unclear in this study system, our results have broad implications for ecology.

Ecological implications

The numerous relationships between crab behavior, physiology and the environment highlight that individual behavior is not likely to be driven by any one factor but regulated by multiple forces acting simultaneously. Our observations indicate that personality may be maintained by a combination of both negative and positive feedback loops. The negative correlation between crab boldness and long–term energy stores is consistent with a negative feedback loop that promotes behavioral differences over the short term, as crabs that build their energy stores are eventually expected to become shy (i.e. the asset protection principle; Clark 1994). Additionally, the positive correlation between crab boldness and size is consistent with a positive feedback loop, as bolder crabs are expected to obtain more resources for growth (Dingemanse and Wolf 2010, Luttbeg and Sih 2010, Sih et al. 2015). This same positive feedback loop may also help foster the observed spatial differences in crab boldness between high– and low– quality reefs, as healthy reefs support larger crabs. Given that linkages between habitat quality and organism size/growth rate are common in terrestrial (Campbell and Campbell 2001, Hamer and McDonnell 2008) and aquatic ecosystems (Chapman and Kramer 1999, Eby et al. 2005, Wilson et al., 2010), such behavioral feedbacks involving the local environment and body size are probably widespread.

In conclusion, our observations suggest that multiple physiological and environmental parameters work in concert to drive animal behavior, and that the strength of these drivers is seasonally dependent. Thus, although our data support ecological theory, this research highlights the importance of evaluating behavior over extended timescales to determine how behavioral variations are regulated. Because numerous forces work simultaneously to influence behavior, evaluating the primary controlling factor(s) behind behavioral differences is likely to remain an ongoing challenge. However, more studies examining both physiological and environmental factors together should bring us closer towards that goal.

ACKNOWLEDGMENTS

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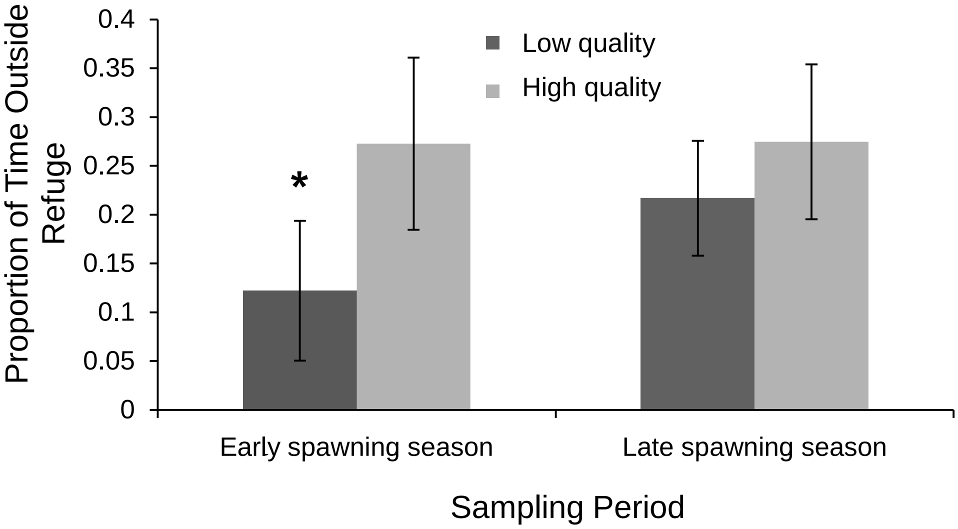

Figure 4.1 Behavior of crabs across habitat quality. Bars represent mean ± SE boldness (proportion of time outside refuge) of mud crabs collected from reefs of low and high quality (N = 5) during the early spawning season and 2 months later (10 crabs collected per reef). Asterisk denotes significant differences.

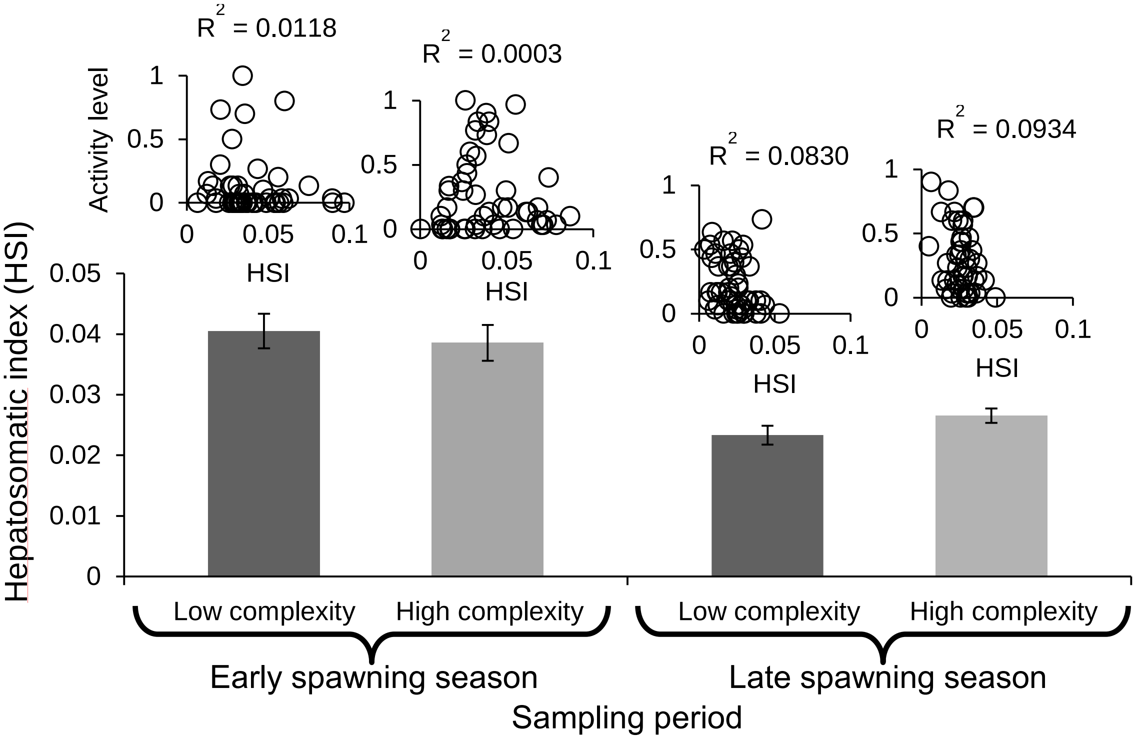

Figure 4.2 Individual behavior as a product of long-term energy stores and the local environment. Bars represent mean ± SE hepatosomatic index (HSI) of mud crabs collected from reefs of high and low quality (N = 5) during the early spawning season and 2 months after (late spawning season). Insets represent individual crab activity level as a function of HSI for each category. Activity level was measured as the proportion of observations where crabs were outside of refuge during 3 h observations. All categories contained 49 individuals, except for crabs collected from low-quality reefs during the late spawning season (N = 50).

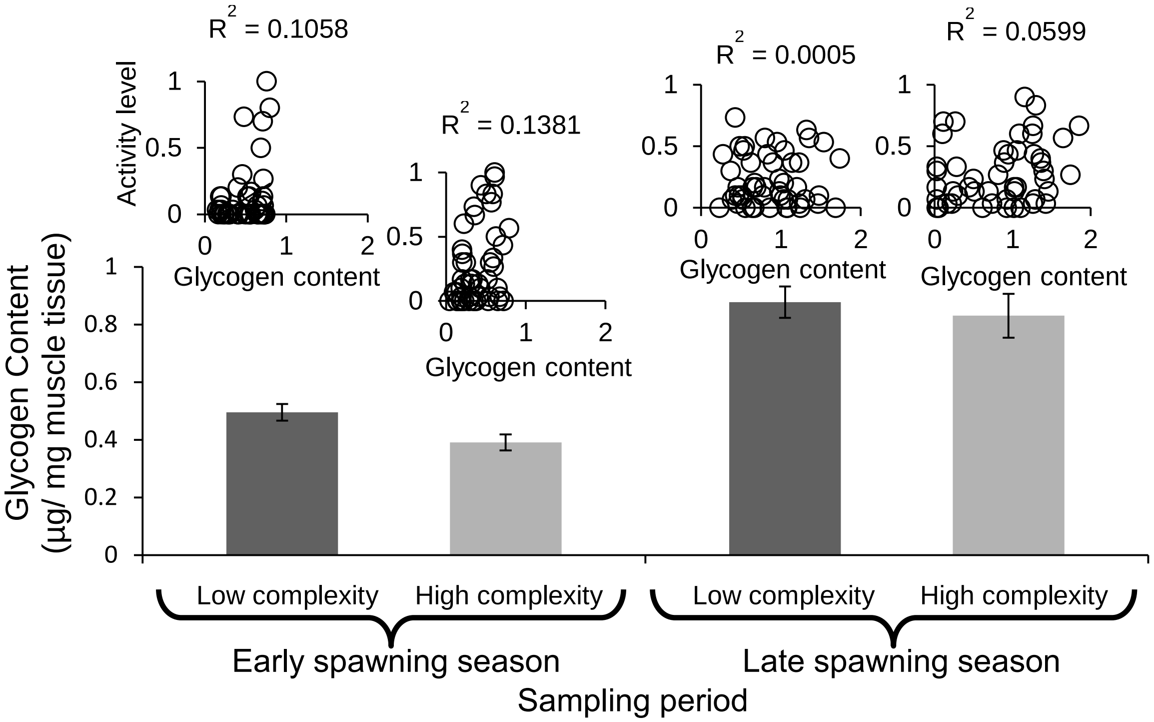

Figure 4.3 Individual behavior as a product of short-term energy stores and the local environment. Bars represent mean ± SE glycogen content (mg/mg muscle tissue) of mud crabs collected from reefs of high and low quality (N = 5) across the spawning season. Insets represent individual crab activity level as a function of glycogen content for each category. Other details are described in the legend of Figure 4.2.

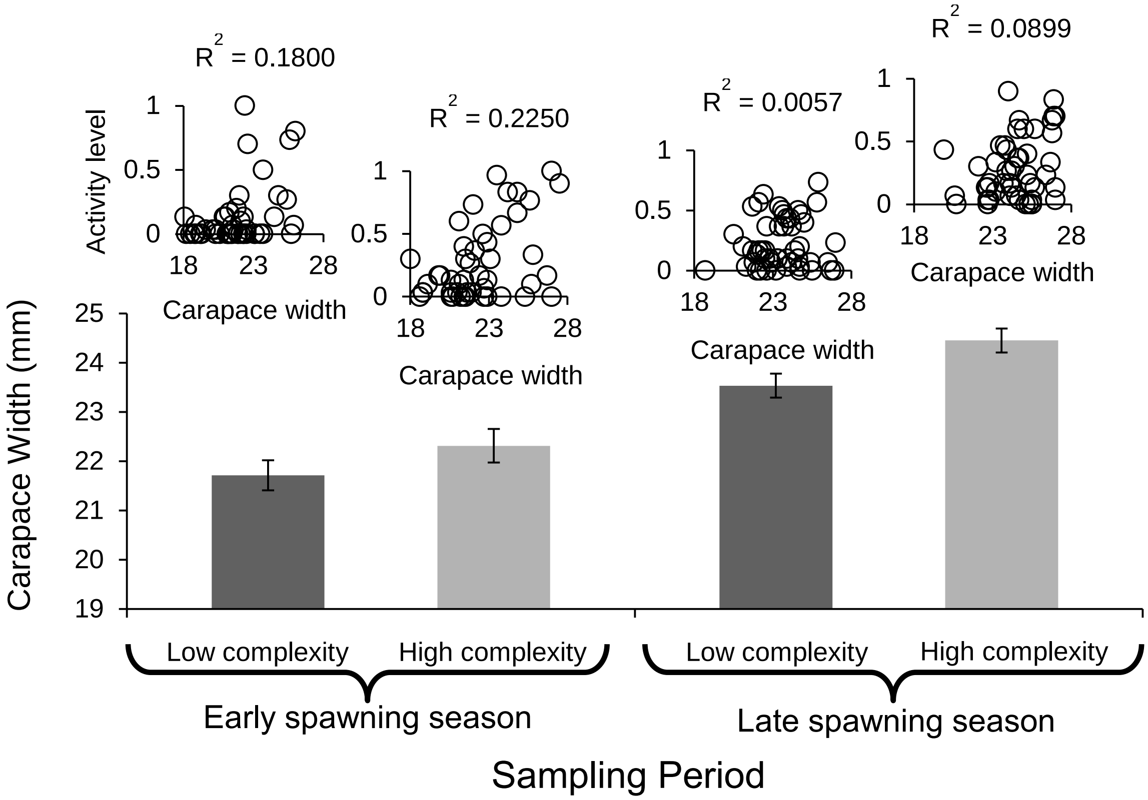

Figure 4.4 Individual behavior as a product of body size and the local environment. Bars represent mean ± SE carapace width (mm) of mud crabs collected from reefs of high and low quality (N = 5) across the spawning season. Insets represent individual crab activity level as a function of carapace width for each category. Other details are described in the legend of Figure 4.2.

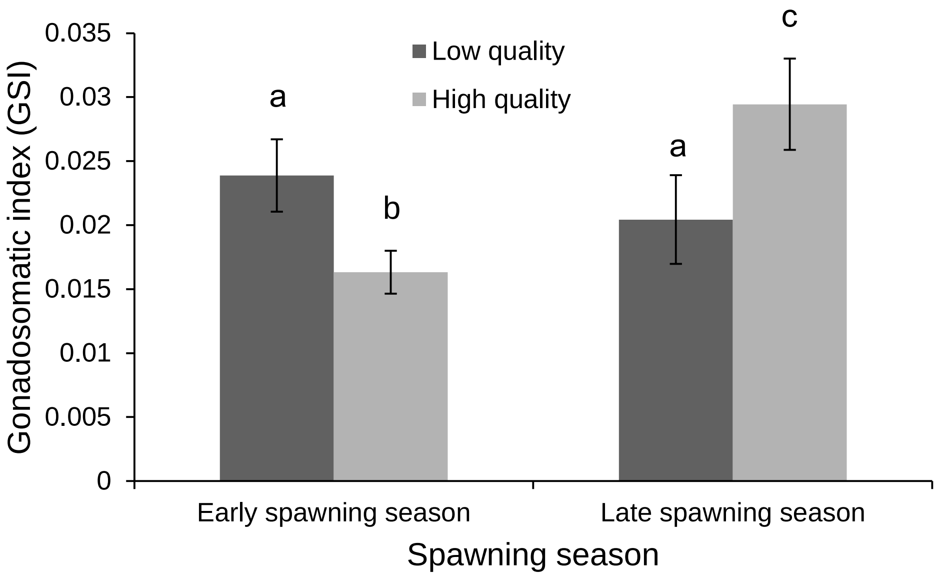

Figure 4.5 Reproductive effort of crabs across habitat quality. Bars represent mean ± SE gonadosomatic index (GSI) from crabs collected at reefs of high quality (N = 49) and low quality (N = 49) during the early spawning season and 2 months later (high quality: N = 49; low-quality: N = 50). Letters above bars represent significant differences.

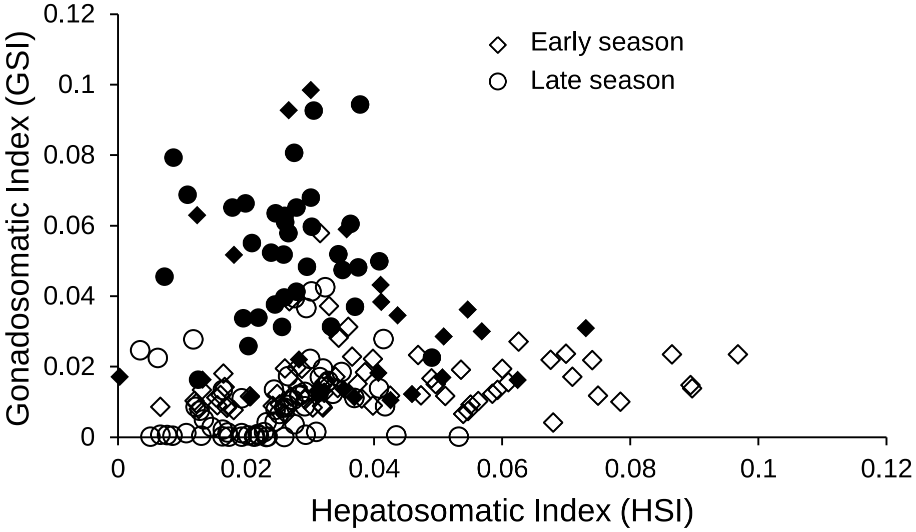

Figure 4.6 Relationship between crab reproductive effort and long-term energy stores. Data points represent individual mud crab gonadosomatic index (GSI) as a function of crab hepatosomatic index (HSI) for individuals taken during the early spawning season (N = 98) and late spawning season (N = 99). Filled symbols indicate vitellogenic crabs.

CHAPTER 5

HABITAT QUALITY MEDIATES PERSONALITY THROUGH DIFFERENCES IN SOCIAL CONTEXT[4]

ABSTRACT

Assessing the stability of animal personalities has become a major goal of behavioral ecologists. Most personality studies have utilized solitary individuals, but little is known on the extent that individuals retain their personality across ecologically relevant group settings. We conducted a field survey which determined that mud crabs, *Panopeus herbstii*, remain scattered as isolated individuals on degraded oyster reefs while high quality reefs can sustain high crab densities (>10/m^2). We examined the impact of these differences in social context on personality by quantifying the boldness of the same individual crabs when in isolation and in natural cohorts. Crabs were also exposed to either a treatment of predator cues or a control of no cue throughout the experiment to assess the strength of this behavioral reaction norm. Crabs were significantly bolder when in groups than as solitary individuals with predator cue treatments exhibiting severally reduced crab activity levels in comparison to corresponding treatments with no predator cues. Personality plasticity depended on the individual. While bold crabs largely maintained their personality in isolation and group settings, shy crabs would become substantially bolder when among conspecifics. These results imply that the shifts in crab

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[4] Belgrad, B.A. and B.D. Griffen. Submitted to *Oecologia*, 2/21/2017.

boldness were a response to changes in perceived predation risk, and provide a mechanism for explaining variation in personality plasticity. Such findings suggest that habitat degradation may produce subpopulations with different behavioral patterns because of differing social interactions between individual animals.

INTRODUCTION

Animal personalities (i.e. consistent differences in individual behavior) are a widespread phenomenon that have been documented in mammals (Réale et al. 2000), birds (Quinn and Cresswell 2005), fish (Huntingford 1976), cephalopods (Sinn and Moltschaniwskyj 2005), spiders (Holbrook et al. 2014), crabs (Toscano et al. 2014b), gastropods (Burrows and Hughes 1991), and other animals (Gosling 2001). Scientists have increasingly acknowledged the importance of animal personalities as these behavioral differences have been linked to numerous ecological processes (Pennisi 2016). At the individual level, personalities can govern survival (Stamps 2007), fecundity (Both et al. 2005), and inter/intraspecific interactions (Holbrook et al. 2014), all of which can regulate population dynamics (Pruitt and Goodnight 2014). In turn, animal personalities can shape community dynamics by influencing the spread of diseases (Barber and Dingemanse 2010, Krause et al. 2010), controlling trophic cascades (Ioannou et al. 2008; Griffen et al. 2012), and have been suggested to facilitate invasion success (Chapple et al. 2012, Carere and Gherardi 2013) and speciation (Wolf and Weissing 2012).

Recent work on animal personalities has focused on understanding the factors which determine personalities and how personalities develop with the goal of predicting individual behavior and its subsequent consequences. Towards this end, behavioral ecologists have begun to examine behavioral reaction norms (Dingemanse et al. 2010), the extent that personalities remain consistent across multiple contexts (e.g. the degree that individuals remain bold/shy while experiencing increasing levels of predator density). Studies on behavioral reaction norms find that there can be considerable individual variation in behavioral plasticity with some population members retaining their original personality across contexts while other members show more behavioral flexibility (Biro et al. 2010, Westneat et al. 2011, Betini and Norris 2012, Dingemanse et al. 2012, Briffa et al. 2013; Biro et al. 2013, Holbrook et al. 2014). However, there are also instances where all individuals display the same personality plasticity across contexts (Carter et al. 2012, Fürtbauer et al. 2015). Despite growing interest in behavioral plasticity, empirical studies that examine this phenomenon remain scarce (Dingemanse and Wolf 2013).

Most personality studies examine solitary individuals. Yet, many animals live in groups, and social context can drastically change as group size fluctuates or conspecific density shifts. The presence of conspecifics can cause behavioral alterations in a number of ways, and social interactions among spiders have been shown to generate persistent personalities (Laskowski and Pruitt 2014). Ecological theory proposes that grouping can both enhance individual behavioral differences (Dall et al. 2004, Hemelrijk and Wantia 2005, Bergmüller and Taborsky 2010) as well as reduce behavioral differences (Conradt and Roper 2003, Sumpter and Pratt 2009) with increases in group size or conspecific density.

Behavioral differences can be enhanced by grouping through competitive interactions and the production of social hierarchies, exemplified by the classic dove-hawk game theory where consistent behavior among aggressive and docile individuals minimizes negative interactions (Smith and Price 1973, Dall et al. 2004). Grouping may also produce behavioral differences by maintaining stochastic differences in initial state (for a detailed explanation see Dall et al. 2004). Alternatively, behavioral differences can be decreased within groups through consensus decision-making. Here, group members can utilize public information on predators, resources, and migration pathways to enhance both individual and group fitness (Krause and Ruxton 2002). Group members in these circumstances can either mimic the behavior of their neighbors, follow a leader, or develop their behavior "democratically" through consensus (Conradt and Roper 2003, Conradt et al. 2009).

Thus, the question arises – to what extent do individuals maintain their personality when in the presence of conspecifics? This question can be exceptionally important for species where group composition or size is not constant, but varies through time. Numerous factors can cause population densities to fluctuate, ranging from species invasions (Didham et al. 2007) to climatic regime shifts (Anderson and Piatt 1999) and habitat degradation (Wilson et al. 2008). Therefore, understanding how organisms alter their behavior to changes in conspecific density can help scientists predict the response of species to these global threats.

Since grouping commonly serves as protection against predators (Krause and Ruxton 2002), the magnitude and stability of the social context behavioral reaction norm can be assessed by measuring the reaction norm under different levels of predation threat. When individuals are alone in the presence of predators, prey activity should be at its lowest to reduce predator exposure whereas in a group context prey can at least partially disregard the predator (e.g. encounter–dilution , Wrona and Dixon 1991) and can simultaneously be stimulated by the presence of conspecifics. Conversely, solitary prey in the absence of predators should not have a strong driving force suppressing their activity. Therefore, the behavioral change across social context should be most extreme in the presence of predators and weakest in their absence.

In this study we examine the mud crab, *Panopeus herbstii*, a species that lives on oyster reefs and that can vary in density more than six–fold as a result of spatial differences in habitat quality (Griffen and Norelli 2015). We have previously shown that this species exhibits a bold–shy continuum of personalities, manifested as refuge use, in the presence and absence of predators, and that these behavioral differences are consistent among individuals for months (Toscano et al. 2014b). The goal of the present study was to determine the extent that personalities remain stable across changes in conspecific density associated with differences in habitat quality. Here, we compared the behavior of the same individuals in isolation and when among cohorts to assess the consistency of individual personality in different ecologically relevant social situations. We also evaluated whether behavioral patterns were maintained in both the presence and absence of predation threat to help evaluate the strength of this behavioral reaction norm. Previous studies have examined the difference in behavior between individuals in isolation versus in group settings (Reebs 2000, Magnhagen and Staffan 2005, van Oers et al. 2005, Webster and Hart 2006, Webster et al. 2007, Magnhagen and Bunnefeld 2009, McDonald et al. 2016). Here we examine this same question, but we take it a step further by linking differences in social context to environmental quality that varies spatially.

METHODS

Reef surveys

We surveyed five high quality and five low quality intertidal oyster reefs within the North Inlet National Estuarine Research Reserve (33°20′N, 79°10′W, Georgetown, SC, USA) to evaluate the distribution of mud crabs, *Panopeus herbstii*, in the field as well as to determine ecologically relevant crab densities to be used in our lab experiment. Reef quality was evaluated by reef height since oyster survival and growth as well as food availability strongly correlates with this parameter (Lenihan and Peterson 1998, Griffen and Norelli 2015). High quality reefs were defined as reefs with heights greater than 20 cm while low quality reefs had heights less than 12 cm. Reef height was calculated as the average of 10 measurements taken at haphazard locations within each reef, each one measuring the height from the tip of oyster clumps to the mud surface (Griffen and Norelli 2015). Crab densities were assessed by haphazardly spacing three 1 m^2 plots throughout each reef and counting the number of mature mud crabs within our sampled size range (17 – 27 mm carapace width). A mixed–effects GLM with a Poisson distribution was used to assess the impact of reef quality on crab density. Reef quality was treated as a categorical explanatory variable and reef identification was treated as a random effect to control for repeated measures made on the same reef.

Experiment overview

We found that crabs were often relatively isolated on low quality reefs and in groups on high quality reefs, so we investigated the individual refuge use of 200 mature mud crabs when in groups versus as solitary individuals. One hundred crabs were observed in the presence of toadfish chemical cues to simulate predation threat while the other hundred crabs had no toadfish exposure as a control. Crabs (mean ± SD carapace width = 24.4 ± 1.8 matching the size of crabs observed during the field survey) were collected by hand from high quality reefs within North Inlet. Our reef surveys described above found that crab density varies with reef quality. Ideally we would run an orthogonal study, but high densities of crabs in low quality reefs are not seen in the natural system. We therefore held reef quality constant at intermediate quality both during collection and while observing behavior to isolate the effects of grouping on personality as we have examined the impact of reef quality on crabs elsewhere (Griffen and Norelli 2015, Chapter 4). All crabs retained both chelipeds and were missing no more than one walking leg. Crabs were transported to the Baruch institute wet lab ~5 km from the sample site where gender was determined by examining the telson (104 females and 96 males). When not under observation, crabs were held inside individual chambers (length 6.5 cm x width 5.0 cm x depth 5.5 cm) submerged within a flow–through system supplied with seawater from the estuary.

Behavior measurements

The following describes our procedure for a single observational block. Ten observational blocks, blocked by time, were run over the duration of the study (August – September, 2015). Five of these blocked trials measured group behavior first, while the other five trials measured solitary crabs first. The order of behavior measurements did not have an effect on individual refuge use (generalized linear model, GLM, $P > 0.05$) so the data were pooled for further analysis. Crabs were collected in two cohorts of 10 individuals during each sampling period (i.e., each blocked trial consisted of 20 crabs). Each cohort of 10 individuals was randomly selected from a single 1 m^2 plot to ensure that natural cohorts of crabs were measured (Chapter 6). One cohort was randomly assigned to a toadfish cue present treatment and the other to a toadfish cue absent treatment. Crabs were fed satiating amounts of ribbed mussel tissue for 1 h upon collection and then starved for 24 h to standardize hunger levels prior to the experiment.

Group refuge use while in cohorts was measured following the behavior assay protocol employed in Chapter 6. Crabs in their natural cohorts were marked with a unique nail polish (Sonia Kashuk) design on their carapace to identify individuals. Cohorts were placed into one of two separate flow–through mesocosms (circular with diameter 1 m; water height 15 cm). Both mesocosms contained ~2 cm of sediment under an ~8 cm layer of cleaned oyster shells covering the entire tank bottom. This composition mimicked the natural structure of reefs and ensured that crabs had ample refuge to hide completely. Thirty scorched mussels were suspended out of reach of the crabs in three mesh containers within each mesocosm to distribute prey odor cues and promote foraging behavior (Griffen et al. 2012). Mesocosms were continuously delivered unfiltered seawater from the estuary. Water entering the predator treatment mesocosm was first pumped through a head tank which contained a mature toadfish (mean ± SD caudal length = 26.8 ± 1.9 cm) to distribute predator odor cues. Toadfish were caught from the estuary by hand no more than two weeks prior to the experiment and fed mud crabs daily to ensure kairomones were produced.

Behavior observations were conducted at night under red light usually beginning between 2000 to 2100 h. Throughout the experiment the observer remained behind a blind to minimize crab disturbance. Crabs were given 10 min to acclimate once cohorts were placed in the mesocosms. After acclimating, we recorded whether each individual crab was exposed on the shell surface layer or hiding underneath the oysters every 6 min for 3 h (30 observations for each crab). Refuge use was measured as the proportion of these 30 observations in which crabs were in refuge and not visible to the observer in the same manner used in previous studies of mud crab behavior (Griffen et al. 2012, Toscano et al. 2014b, Chapter 4). Following this first behavioral treatment, crabs were again fed satiating amounts of ribbed mussels and starved for 24 h before commencing the second behavioral treatment (grouped or solitary).

Crab refuge use as solitary individuals was measured following the behavior assay protocol of Griffen et al. (2012). Each crab was placed in an individual plastic mesocosm (length 40 cm; width 22 cm; water height 15 cm) with a ~2 cm sediment layer covered by an ~8 cm oyster shell layer. Nine mussels were suspended in a mesh container out of reach of the crabs. The number of mussels and oyster shells used corresponded to the same density of mussels and shells per volume water used in the group behavior assay. Water from the estuary was continuously supplied to the mesocosms via a flow–through system. Crabs which were initially assigned to predator cue present treatments again had their water pumped through a head tank with a toadfish to deliver odor cues. Thus, individuals assigned to a predator treatment had their behavior assayed both in solitary and group contexts, but individuals never experienced both predator treatments. Observations of individual crab behavior in isolation were conducted in the same manner as described above for individual behavior with a group. We examined the effect of conspecific and predator presence on crab behavior (i.e., proportion of time spent active) using a mixed–effects GLM with a binomial distribution (fit by restricted maximum likelihood (REML) following the protocol of Zuur et al. 2009; R package: *lme4*). We treated grouping status (i.e. in cohort or solitary), predator treatment, gender and the covariate carapace width as fixed effects. Individual crab identification nested within observational block were treated as random effects to control for repeated measures of each individual crab and for non-independence of crabs within the same trial. We started with the full model and stepwise removed nonsignificant interaction terms with the highest *P* values, retaining the interaction between carapace width and grouping status as well as the interaction between carapace width and predator treatment. This and all other analyses were conducted using R v.3.0.3 (R Development Core Team, 2015). All applicable institutional and national guidelines for the care and use of animals were followed.

Behavioral reaction norm analysis

We tested whether crabs exhibited behavioral reaction norms across social contexts using mixed–effects random regression models estimated by REML following Dingemanse et al. (2010) and Kluen and Brommer (2013). The variables grouping status, predator treatment, gender, carapace width and the associated interactions involving carapace width were treated as fixed effects to ensure that variance from these variables did not end up in the random effect variance. A random intercept model was compared to a random intercept and slope model using the Akaike information criterion (AIC) to assess whether individuals differ in their plasticity. Here, statistical support for the inclusion of random slopes signifies individuals differ in their responses across social status while covariance between the intercept and slope indicates the relationship between crab personality and their behavioral plasticity across an environmental context. Confidence intervals around the random regression estimates of intercept, slope, and their correlation were calculated by nonparametric bootstrapping of the random intercept and slope model.

RESULTS

Reef surveys

The density of mature crabs on reefs varied from 0/m^2 to 12/m^2. Crab densities on high quality reefs were on average nearly six times higher than on low quality reefs (GLM; estimate = 1.76, Z = 6.51, $P < 0.0001$; Figure 5.1).

Behavioral measurements

Crabs were substantially more active in the presence of conspecifics than in isolation (Table 5.1). Crabs were also significantly less active in the presence of predator cues than in the absence of such cues (Table 5.1). Further, the influence of grouping varied with the presence of predator cue so that grouping crabs together in the presence of predators caused crab refuge use to decrease on average by 74% whereas grouping in the absence of predators only elicited a 43% decrease in refuge use (Figure 5.2). The main effect of carapace width did not influence activity level (Table 5.1). However, there was a significant two–way interaction between carapace width and social context (Table 5.1) as well as between carapace width and predator treatments (Table 5.1). This is probably because crab refuge use slightly decreased with increasing carapace width, particularly when crabs were isolated (Figure 5.3a,b) or exposed to predator odor cues (Figure 5.3a,c). Gender did not influence crab activity levels (Table 1).

Behavioral reaction norm

There was a considerable amount of individual variation in crab activity levels as some crabs were always active during the study while others hid the entire time (individual ID produced 43% of model variance; Table 2). Inclusion of random slopes in the random effects model substantially enhanced model fit (ΔAIC = 492) indicating that crabs did not increase in refuge use equally across social context. In fact, there was a negative correlation between solitary behavior and behavioral plasticity across social context (correlation between estimated intercepts and slopes = –0.73; Table 5.2) While solitary bold individuals would typically remain bold when placed in groups, solitary shy individuals frequently did not remain shy, but would cease using refuges when grouped (Figure 5.4).

DISCUSSION

Our findings demonstrate that social context has a large impact on individual behavior, and suggest that changes in habitat quality can produce the behavioral differences documented above by altering the density of populations. Additionally, we found that personality plasticity varies substantially among individuals. Although crabs would often maintain their relative personality in isolated and group settings, such that bold and shy individuals when alone were also the bold and shy members when together, the behavior of some individuals was shaped by the group more than others. This pattern was observed both in the presence and absence of predation threat which indicates that the behavioral differences between isolated and group settings are relatively stable. These results support theoretical predictions on behavioral reaction norms (Dingemanse et al. 2010, Dingemanse and Wolf 2013), and highlight the role of conspecific density in community dynamics.

Crab densities naturally ranged from asocial settings with isolated individuals scattered across oyster reefs to social settings with crab densities exceeding those used in this study. Consequently, the behavioral differences documented here are probably common in the wild. Since these crab densities corresponded to reef quality, low and high quality reefs potentially produce drastically different behavioral patterns independent of differences in refuge provided by differences in structural complexity. Indeed, in our previous study that observed crabs from different quality reefs in a common garden experiment, we found that individuals from high quality reefs were bolder than those from low quality reefs (Chapter 4), even when crabs were measured in isolation. These findings indicate that reef degradation may exacerbate changes in behavior and community processes by altering population densities.

Crab boldness likely increased in group settings because the presence of conspecifics in the vicinity reduces the risk of predation either by enhancing predator detection (i.e. many–eyes effect, Treherne and Foster 1980) or by reducing the encounter rate between an individual crab and predator (e.g. encounter–dilution, Wrona and Dixon 1991; predator swamping, Sweeney and Vannote 1982). This conclusion is further supported by the decrease in boldness between crabs in the presence of predator cues versus their absence for both social contexts. However, crab boldness may have partially increased due to antagonistic interactions between individuals although multiple individuals are known to naturally cohabit the same oyster cluster. Interestingly, mean crab boldness under predation threat in the presence of conspecifics matches mean boldness when isolated without predator cues. Higher crab boldness has previously been demonstrated as a causative factor leading to higher mussel consumption (Griffen et al. 2012) and mortality rates (Chapter 6) in this system. Thus, higher conspecific densities may allow crabs to boost their foraging in the presence of predators while maintaining levels of perceived predation risk similar to solitary individuals in the absence of predators. In this way, fluctuations in conspecific density or grouping may not only change consumption rates in an area by altering the number of individuals foraging, but also by altering how much each individual forages.

We found that bold crabs mostly retained their personality throughout the study while shy crabs displayed high behavioral plasticity, becoming substantially bolder when among cohorts. Shy crabs likely showed more behavioral plasticity than bold individuals across social context because of differences in perceived predation risk between solitary and group contexts. Individuals who are bold in isolation with relatively high perceived predation risk would naturally remain bold in a group context with lower perceived predation risk whereas individuals who are shy when solitary can afford to become bolder in the presence of conspecifics. Crab boldness is also known to correlate with individual carapace width under predation threat (Toscano et al. 2014b) as larger crabs are not as vulnerable to gape–limited predators such as toadfish (observed among other crab species; Hill 2011, Heinonen and Auster 2012). This additional size refuge from predation in large crabs may partially explain why larger, bolder group members would remain bold when isolated and ignore differences in perceived predation risk across social context. Similar personality shifts in social contexts have also been reported with perch (Magnhagen and Bunnefeld 2009) and killifish (McDonald 2016), although comparisons between size or predator presence were not made. Such a trend between personality, behavioral plasticity, and size exposes a potentially powerful tool for predicting individual behavior across multiple contexts.

Ecological implications

The results presented here have two broad implications for community dynamics. First, our findings indicate that consumer interactions are more complex than commonly assumed. Ecological models generally assume that consumers either have antagonistic effects (i.e. predator interference, Skalski and Gilliam 2001) or help each other (e.g. group hunting, Handegard et al. 2012). Crabs are notoriously antagonistic towards each other (Hazlett 1968, Jachowski 1974, Vazquez Archdale 2003, Griffen and Williamson 2008, Milner et al. 2010). However, we show that even for aggressive species such as crabs, grouping under predation threat can cause individuals to spend more time active/feeding than they would in isolation without that threat demonstrating that predators which are often antagonistic towards each other can still facilitate foraging by grouping together. This suggests that antagonism vs facilitation effects on functional response curves may be too simplistic a perspective (e.g. Hassell and Varley 1969, Beddington 1975, DeAngelis et al. 1975, Crowley and Martin 1989), as some systems may experience both antagonistic and facilitative effects simultaneously from the same process.

Secondly, fluctuations in population density are a widespread response to changes in habitat quality (Heck Jr and Wetstone 1977, Levin 1993, Warren et al. 2001, Goode et al. 2005, Gratwicke and Speight 2005, Cushman, 2006), and likely produce similar behavioral shifts in other species since heightened individual boldness is a typical reaction to increases in conspecific density (Reebs 2000, Magnhagen and Staffan 2005, van Oers et al. 2005, Webster and Hart 2006, Webster et al. 2007, Magnhagen and Bunnefeld 2009, McDonald et al. 2016). However, as this and other studies have shown, not all individuals display the same level of behavioral plasticity across social context (van Oers et al. 2005, Kralj-Fišer et al. 2007, Magnhagen and Bunnefeld 2009, Oliveira 2009, McDonald 2016). Such behavioral differences are important because they can govern how well individuals adapt to social and environmental changes. Individual success is largely dependent on behavior as boldness correlates with mortality rates (Godin and Davis 1995, Bremner-Harrison et al. 2004, Stamps 2007, Chapter 6), fecundity (Janczak et al. 2003, Both et al. 2005, Wilson et al. 2010, Bridger et al. 2015), and physiological condition (Johnson and Sih 2005, Chiba et al. 2007, Mas-Muñoz et al. 2011, Chapter 4) in numerous systems. Since the advantages and disadvantages of boldness do not remain the same across different environmental contexts, individual differences in behavioral plasticity will cause some individuals to be more impacted by these environmental changes than others (e.g. disproportionate alterations in energy intake, predation risk, and mating success).

In general terms, individuals may either retain their personality after an environmental change or alter their behavior (Figure 5.5a,b). However, these two outcomes will have unequal consequences for individual fitness since a personality which is best suited for one environment may not be optimal in another environment (Figure 5.5c,d). Two alternative scenarios are possible under these circumstances. In the first scenario, individuals which do not alter their behavior after the environmental change may start living in an environment that is better suited for their personality (Figure 5.5a, individual 1, environment 2). While these stable personality individuals may slightly increase their fitness under this scenario (Figure 5.5c, individual 1), behaviorally plastic individuals would not be expected to have the same increase in fitness (Figure 5.5c, individual 2). This is because there may be costs to behaviorally plastic individuals altering their behavior as well as disproportionate gains from matching their behavior with the stable personality individuals (Figure 5.5c, shaded cone). Alternatively, the new environment (environment 2) might be less suited for the personality type of the behaviorally stable individuals (Figure 5.5, individual 1). Under this scenario, behaviorally plastic individuals would be unlikely to match their behavior to the behavior of the stable individuals because this would cause decreases in fitness. Instead, these behaviorally plastic individuals would likely further separate their behavior from the stable individuals (i.e. behavioral divergence Figure 5.5b). Thus, these stable individuals would be expected to decrease in fitness while the behaviorally plastic individuals would exhibit gains in fitness (Figure 5.5d). The frequency that species exhibit such personality dependent variation in behavioral plasticity remains unknown due to the low number of studies examining behavioral reaction norms. However, studies quantifying this phenomenon across different contexts may therefore yield insights into which individuals are most at risk or impacted by environmental disturbances.

In conclusion, we have shown that mud crabs alter the expression of their personality in response to the density of conspecifics and tied these differences to habitat quality. Based on the arguments above, this can have far-reaching implications for this and potentially other systems. The results of this study demonstrate that common changes in social context play a large role in structuring individual behavior which may be extended to a wide variety of study systems. Our findings underscore the importance of conducting experiments at ecologically relevant conspecific densities.

ACKNOWLEDGMENTS

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Table 5.1 Descriptive statistics of a mixed-effects generalized linear model examining the impact of social context, predator presence, carapace width, and gender on crab activity levels.

Fixed Effect	**Estimate**	**SE**	**Z**	***P***
Social Context	1.94	0.43	4.56	<*0.0001*
Predator Presence	4.10	1.50	2.73	*0.0064*
Carapace Width	0.01	0.02	0.57	0.5706
Gender	-0.07	0.16	-0.46	0.6451
Carapace Width X Social	0.05	0.02	2.71	*0.0068*
Carapace Width X Predator Presence	0.13	0.06	2.11	*0.0348*

Table 5.2 Variance components from a mixed-effects random regression model testing for differences between individuals ("Individual ID") and for random slope variation across individuals between solitary and group settings ("Individual x Social Context") blocked across trial.

Random Effect	**Variance**	**Correlation**	**CI (95%)**	**%**
Individual ID	2.38		0.79 – 3.14	42.8
Individual X Social Context	2.00		0.75 – 3.58	36.0
Trial	0.17		0.10 – 0.85	3.1
Residual	1.00		0.82 – 1.24	18.1
Correlation between Intercept and slope		-0.73	-0.92 to -0.37	

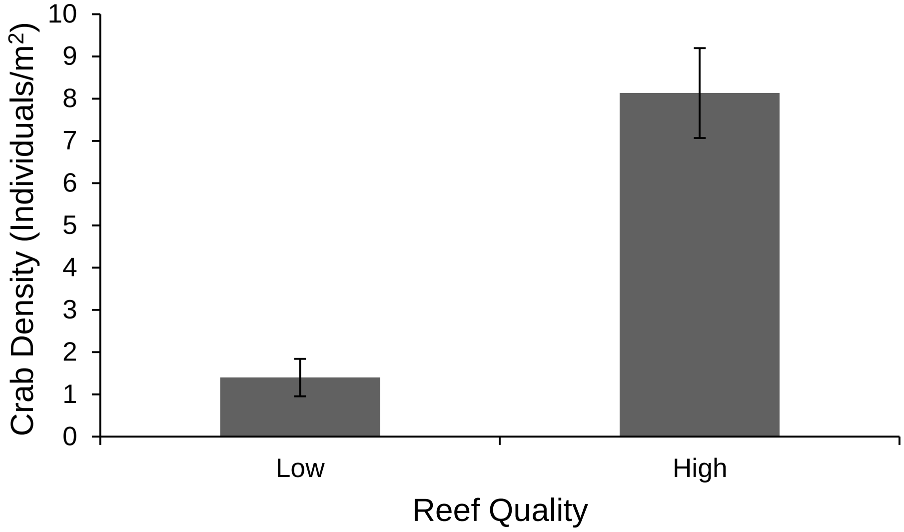

Figure 5.1 Mean ± SE crab density (individuals/m^2) within degraded (n = 5) and healthy oyster reefs (n = 5).

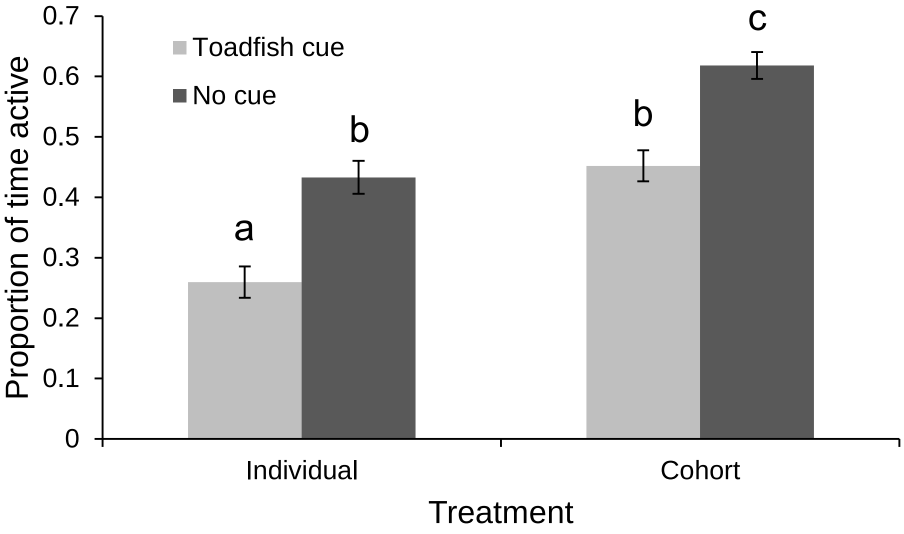

Figure 5.2 Mean ± SE proportion of time crabs spent active outside of oyster refuges when in natural cohorts versus separated as solitary individuals. Crabs were either exposed to predator odor cues from toadfish (n = 100) or a control of no cue (n = 100). Crabs measured in cohorts and as isolated individuals were the same crabs.

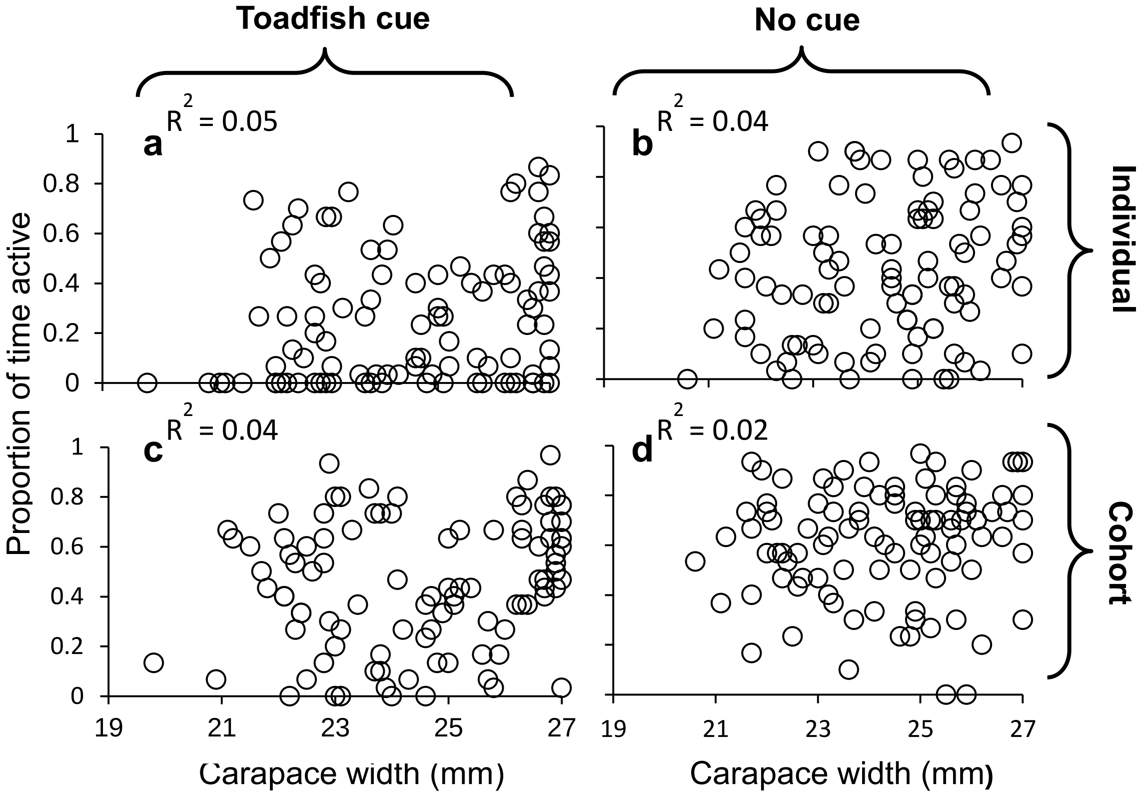

Figure 5.3 Individual crab activity levels as a function of carapace width (mm) when in isolation (**a** and **b**) and in natural cohorts (**c** and **d**). Crabs were either exposed to predator odor cues (n = 100; **a** and **c**) or a control of no cue (n = 100; **b** and **d**).

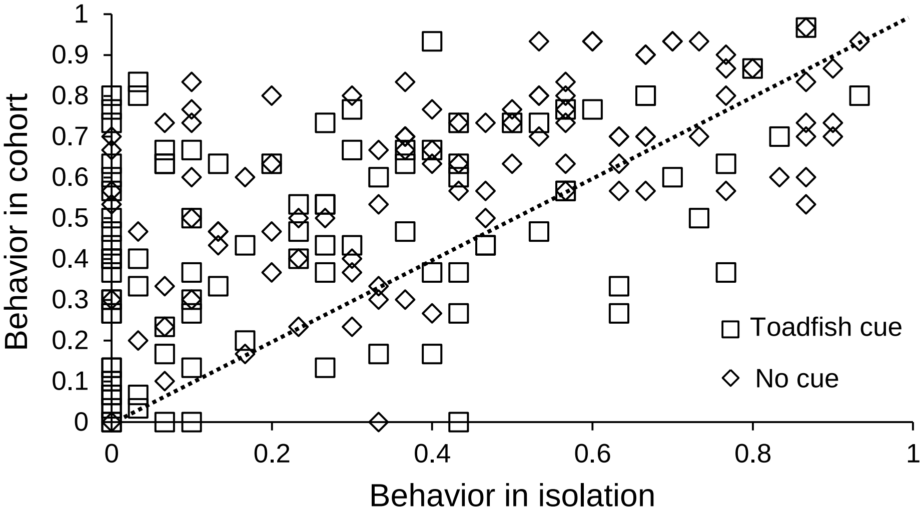

Figure 5.4 Individual crab activity levels when in natural cohorts of ten as a function of their behavior when in isolation. Crabs were either exposed to predator odor cues (n = 100) or a control of no cue (n = 100). Dotted line indicates perfect behavioral consistency.

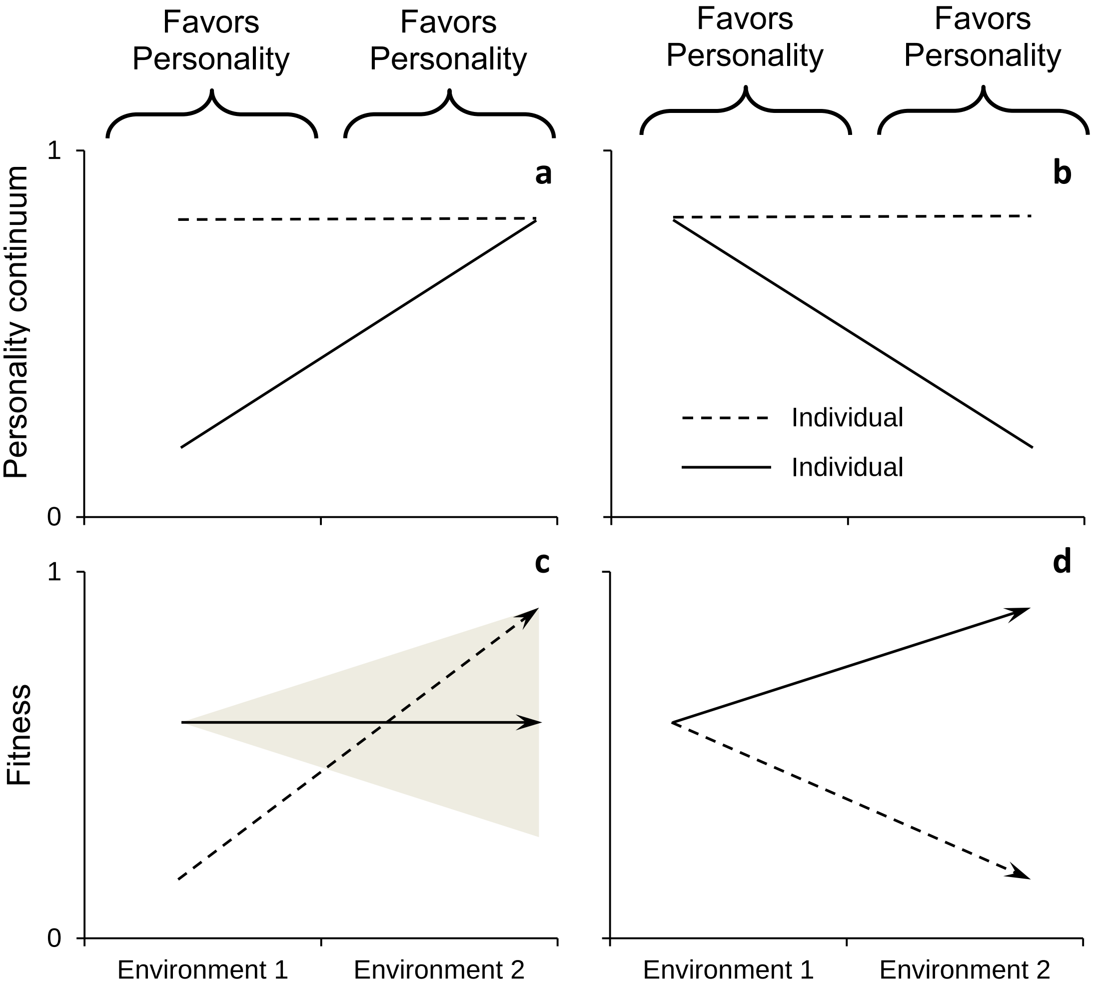

Figure 5.5 Idealized depiction of personality-dependent behavioral plasticity with environmental changes that produce behavioral convergence **(a)** and divergence **(b)** as well as the associated change in fitness between individuals (**c** and **d** respectively). Lines represent individuals with the Y-intercepts depicting initial personality/fitness and the slope depicting the change in behavior **(a,b)** or fitness **(c,d)** across the environmental gradient. Shaded cone represents possible changes in fitness for behaviorally plastic individuals due to environmental changes coupled with possible fitness costs and benefits for altering behavior.

CHAPTER 6

PREDATOR–PREY INTERACTIONS MEDIATED BY PREY PERSONALITY AND PREDATOR HUNTING MODE[5]

ABSTRACT

Predator–prey interactions are important drivers in structuring ecological communities. However, despite widespread acknowledgement that individual behaviors and predator species regulate ecological processes, studies have yet to incorporate individual behavioral variations in a multipredator system. We quantified a prevalent predator avoidance behavior to examine the simultaneous roles of prey personality and predator hunting mode in governing predator–prey interactions. Mud crabs, *Panopeus herbstii*, reduce their activity levels and increase their refuge use in the presence of predator cues. We measured mud crab mortality and consistent individual variations in the strength of this predator avoidance behavior in the presence of predatory blue crabs, *Callinectes sapidus*, and toadfish, *Opsanus tau*. We found that prey personality and predator species significantly interacted to affect mortality with blue crabs primarily consuming bold mud crabs and toadfish preferentially selecting shy crabs. Additionally, the strength of the predator avoidance behavior depended upon the predation risk from the predator species. Consequently, the personality composition of populations and predator hunting mode may be valuable predictors of both direct and indirect predator–

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[5] Belgrad, B.A. and B.D. Griffen. *Proceedings of the Royal Society B: Biological Sciences*. 283: 20160408. Reprinted here with permission of publisher.

prey interaction strength. These findings support theories postulating mechanisms for maintaining intraspecies diversity and have broad implications for community dynamics.

INTRODUCTION

The role of predation is critical in shaping ecosystem structure and function (Berger et al. 2001, Hawlena and Schmitz 2010). Predator–prey interactions can alter community composition (Kneite and Chase 2004), mediate trophic cascades (Mooney et al. 2010), increase biodiversity (Letnic and Ritchie 2012), and affect species invasions (Snyder et al. 2004). Furthermore, predators can control the dynamics of prey populations by influencing such aspects as survival (Skelly 1994), growth (Peckarsky et al. 1993), behavior (Werner et al. 1983), size structure (Hall et al. 1976), and distribution (Beauchamp et al. 2007); while prey can likewise regulate predator populations (Yoshida et al. 2003, Ishii and Shimada 2010). One of the primary components of predator–prey interactions is the behavior and subsequent survival of prey in the presence of predators.

For decades, scientists have studied the behavioral response of prey to predators. Numerous studies have directly linked prey activity levels (e.g. Skelly 1994, McIntyre et al. 2012) and refuge use (e.g. Colishaw 1997, Belgrad and Smith 2014) to predation risk, while other investigations have determined that predator avoidance behaviors (e.g. migration, reduced foraging) can limit prey growth (Werner et al. 1983), development (Skelly and Werner 1990), and fecundity (Peckarsky et al. 1993). These behavioral changes also have an enormous impact on the natural community. Shifts in the distribution of prey to avoid predators can alter competitive interactions between different prey species (Lima 1998), whereas reduced foraging by prey in response to predation risk can reverberate across trophic levels (Grabowski and Kimbro 2005, Griffen et al. 2012).

Owing to the importance of predator avoidance behaviors in structuring ecological communities, ecologists seek to uncover the factors that determine the strength, variation, and effectiveness of these behaviors in order to predict community and population dynamics. Towards this end, studies have concentrated on identifying the respective roles that biological and environmental variables play in shaping these behavioral changes. For instance, studies have documented predator avoidance behaviors varying by such factors as parasitic infection (Belgrad and Smith 2014), environmental contamination (Weis and Candelmo 2012), predator species (Vilhunen and Hirvonen 2003), and even predator diet (Persons et al. 2001). Nevertheless, despite advances in our ability to qualitatively predict the response of prey to predators (Schmitz 2005), our knowledge remains limited on the effectiveness of predator avoidance behaviors in promoting survival because of the wide range of responses prey may exhibit and the myriad ways predators can respond to these behaviors.

Recently, there has been growing recognition of the importance of animal personality in mediating predator–prey interactions (Griffen et al. 2012, Pruitt et al. 2012, DiRienzo et al. 2013). Animal personalities are a widespread phenomenon across the animal kingdom where individuals consistently exhibit different behavior types (Bell and Sih 2007, Biro and Stamps 2008, Brodin et al. 2013). While prey often seek refuge or reduce their activity in the presence of predators, every member in a population does not produce the same magnitude of a response. Instead, some individuals can be bold and spend the majority of their time active in risky, energetically advantageous locations, while other individuals may be shy and stay in habitats which provide refuge, but not opportunities to forage. These differences in personalities not only probably affect their chances of overall survival, but may also alter the species of predator from which they are at risk, as different predators use different habitats and hunting modes (e.g. larval fish which migrate to shallow water to avoid aquatic predators may expose themselves to terrestrial predators; Crowder et al. 1997). Despite the frequency with which prey encounter multiple predators in the natural environment (Cohen and Briand 1984, Schoener 1989), only one study to our knowledge has examined the interactive effects of prey personality and predator species on predation risk (Blake and Gabor 2014).

Studies which attempt to predict prey responses to multiple predator species have theorized that predator avoidance behaviors should be the strongest in the presence of cues from sit–and–wait (ambush) predators, as detection should be more indicative of impending predation than cues from active hunters which are dispersed widely and encountered frequently (Preisser et al. 2007, Schmitz 2010, Miller et al. 2014). However, to date there have been few studies that have explored the relationship between predator hunting mode/domain and prey mortality (e.g. Carey and Wahl 2010, Carey Wahl 2011, Miller et al. 2014), and none that have incorporated prey personality. Here, we examine the interactive roles of prey personality and predator hunting mode in governing predation risk within a simple food web.

METHODS

Study system

We studied a food web which is prevalent within intertidal salt marsh ecosystems along the Atlantic and Gulf coasts of North America. This system consists of blue crabs, *Callinectes sapidus*, and toadfish, *Opsanus tau*, as top predators, the mud crab, *Panopeus herbstii*, as an intermediate predator, and the scorched mussel, *Brachidontes exustus*, as prey. Blue crabs and toadfish are abundant predators that commonly inhabit oyster reefs along the Atlantic coast (Gudger 1910, Williams 1974). While blue crabs are opportunistic foragers which actively search for prey (approx. 34% of diet consists of other crabs; Reichmuth et al. 2009), toadfish are ambush predators which feed predominantly on mud crabs (77% of diet in South Carolina; Wilson et al. 1982). In turn, mud crabs strongly reduce their activity levels and increase their time in refuge in response to different predators (Hughes et al. 2014), and exhibit a bold–shy continuum of personality types (Griffen et al. 2012, Toscano et al. 2014b). Thus, ecological theory predicts that mud crabs should have an elevated predator avoidance response and higher predation risk in the presence of toadfish than blue crabs (Preisser et al. 2007, Schmitz 2010). This theory was tested by using cohorts of animals that were sequentially moved through two experiments. The first experiment measured the personality of individual mud crabs when assessed together as naturally occurring cohorts in the presence of a specific type of predator. The second experiment measured the mortality risk of that same predator on each of these same mud crabs as a consequence of their individual personality type.

Refuge use in the presence of different predator odor cues

We performed an experiment to assess the proportion of time individual mud crabs spend active versus hiding in refuge in the presence of predator odor cues from either a single toadfish, a single blue crab or control conditions with no predator cue. Previous work in our laboratory determined that differences in this behavior between individuals persist over months (Toscano et al. 2014b), are consistent across a range of conditions (i.e. predator present/absent, Griffen et al. 2012; changes in conspecific density, Chapter 5; starvation level (B.A. Belgrad 2015, unpublished data)), and are correlated with individual energetic strategies (Toscano and Monaco 2015). We collected 300 mature mud crabs that were not missing any limbs (mean ± SD carapace width = 24.1 ± 2.2 mm) by hand from intertidal oyster reefs within the North Inlet National Estuarine Research Reserve (33°20′N, 79°10′W, Georgetown, SC, USA). Crabs were collected in three cohorts of 10 individuals during each of 10 blocked sampling periods (i.e. each blocked trial consisted of 30 crabs total). Individuals were randomly selected from 1 m^2 plots to ensure that natural cohorts of 10 crabs were measured. Crab gender was identified by examination of the telson (167 males and 133 females). Crabs were starved for 24 h and the carapace of each was marked with a unique nail polish (Sonia Kashuk) design to identify individuals. Preliminary work determined that these markings did not alter crab behavior. Cohorts were randomly assigned a predator cue treatment and placed into one of three separate flow–through mesocosms (circular with diameter 1 m; water height 15 cm). Each mesocosm contained approximately 2 cm sediment under an approximate 8 cm matrix of cleaned oyster shells covering the entire tank bottom. This composition mimicked the natural structure of reefs and ensured that crabs had ample refuge to hide completely. Thirty scorched mussels were distributed in three mesh containers within each mesocosm outside the reach of crabs to continuously stimulate foraging behavior (Griffen et al. 2012). Flow–through mesocosms were supplied with water from the estuary which was first pumped through a head tank. The head tank for each mesocosm contained either a mature toadfish (caudal length ± SD = 28.4 ± 2.8 cm), blue crab (carapace width ± SD = 14.8 ± 0.6 cm), or no predator depending on the predator odor cue treatment. Predators were caught from the estuary by dip net no more than one week prior to the experiment and fed mud crabs each day to ensure kairomones were produced. We conducted all experimental trials at night under red light following the observational procedures of (Griffen et al. 2012, Toscano et al. 2014b) to ensure mud crabs were at their most active and were undisturbed by the observer.

Crabs were tested in trials consisting of one cohort per treatment (toadfish, blue crab, no predator) with six days separating the commencement of each trial. All trials began between the hours 20.00 and 21.00, and once cohorts were placed in the mesocosms, crabs were given 10 min to acclimate. After acclimating, we recorded whether crabs were actively exposed on the surface of the shell layer or were taking refuge underneath the shells at 6 min intervals for the next 3-h. The proportion of these 30 observations in which crabs hid in refuge and were not visible to the observer was used as our response variable. We examined the effect of predator presence on crab behavior using a mixed–effects generalized linear model (GLM) with a binomial distribution (R package: *lme4*). We treated predator treatment, gender, and the covariate carapace width as fixed effects and trial as well as individual crab identification as random effects to control for non–independence of crabs within the same trial and for repeated measures of each individual crab. This and all other analyses were conducted using R v3.0.3 (R Development Core Team, 2015).

Effect of mud crab personality on predation risk

Immediately after observing crab behavior (described in the last subsection), we used the same crab cohorts to assess whether crab predation risk was influenced by the proportion of time individual crabs spend in refuge within oyster shells and by predator species. We assigned crabs the same predator treatment they experienced previously to keep cohorts intact throughout the entire study. Crabs were fed a satiating amount of fish (*Fundulus heteroclitus*), marked with individually numbered bee tags (queen marking kit: the Bee Works, Orillia, Ontario, Canada), and starved for 24-h. After the starvation period, the cohorts were placed into one of three large flow–through mesocosms diameter 2 m; water height 90 cm). Each mesocosm contained approximately 2 cm of sediment underneath four clusters of live oysters (length approx. 38 cm, width approx. 31 cm and height approx. 28 cm) which were standardized by weight (15.000 kg within less than 0.1%). Oysters were collected from the estuary and cleaned of any inhabiting crabs. Scorched mussels naturally attached to these collected oysters were standardized by number of individuals (within 8.3%) and served as the mud crabs' food source to mimic natural conditions.

During each blocked trial (n = 10), a single toadfish, blue crab, or no predator (to serve as a control for cannibalism) was placed in each mesocosm depending on the experimental treatment. Each trial used new predators, but we used the same individual predators which provided odor cues in the previous behaviour experiment as predators within the large mesocosms to ensure prey behavior remained consistent. Predators were starved 24-h to standardize hunger levels and placed in the mesocosms 10 min prior to the mud crabs to ensure kairomones were distributed throughout the tank (no crabs were lost to predation during introduction into the tanks). Mud crab survival was checked daily for seven consecutive days to determine which individuals were consumed. This was done by removing all the oyster clumps and thoroughly raking the sediment. No additional crabs were consumed until at least 10 min after the sediment had been raked (length of observation). Any missing crabs were presumed dead as there was no way for crabs to escape and remnants of missing animals were often found. We assessed whether crab mortality was influenced by the fixed effects of predator species, and the covariates crab refuge use (measured in the first experiment), and crab size using a mixed–effects Cox proportional hazards model (i.e. a survival analysis) with trial as a random effect (R package: *frailtyHL*). This model allowed us to right censor the data to account for crabs that were not consumed by the end of the trial. A Cox proportional hazards analysis is a statistical model which recognizes that the highest values in a study may simply be the maximum possible value, because a result did not occur by the end of the observation period, so the model weighs the data points accordingly (i.e. the data are right censored). We also conducted a two–sample Kolmogorov–Smirnov test to compare the distribution of mud crab personality types consumed by blue crabs and toadfish.

Predator behavior

We monitored predator behavior during five of the 10 experimental trials described in the previous section to determine the hunting strategies of blue crabs and toadfish, and to assess whether hunting strategy could potentially explain the preferential consumption of bold or shy crabs. We examined two aspects of predator hunting behavior: predator location and movement within the mesocosms. These were each recorded every hour between 7.00 and 22.00 (20 observations) during the second and fifth day of the trial, and then data from these two time periods were combined for analyses. We analyzed proportion of time within versus outside of oysters and proportion of time moving versus stationary using two separate mixed–effects GLMs with a binomial distribution, using predator species as a fixed effect and trial block treated as a random effect.

RESULTS

Refuge use in the presence of different predator odor cues

The presence of a predator cue caused mud crabs to spend significantly more time in the refuge of oyster shells (predator absence, estimate ± SE ± 1.26 ± 0.19, Z = 6.74, *P* < 0.0001; Figure 6.1). In controls with no predator cue, crabs only spent, on average, 32% of their time under shells with crabs substantially altering their refuge use depending on the predator species so that crabs hid 47% of the time when exposed to toadfish cues and 57% of the time in the presence of blue crab cues (comparison between predators: toadfish versus blue crab presence, estimate ± SE = 0.47 ± 0.19, Z = 2.50, *P* = 0.0125; Figure 6.1). There was a large amount of individual variation (i.e. differences in personality) across all predator treatments in the proportion of time crabs spent hiding rather than actively foraging, with some individuals spending 100% of their time in refuge while others hid for 0% of the time (variance in time by treatment: blue crab = 5%, toadfish = 7%, control = 6%). Conversely, crab behavior did not vary greatly with experimental trial (variance, 0.001). Both carapace width and gender also had negligible effects on crab behavior (estimate ± SE = –0.03 ± 0.03, Z = –1.04, *P* = 0.2988; estimate ± SE = –0.10 ± 0.15, Z = –0.64, *P* = 0.5197, respectively).

Effect of mud crab personality on predation risk

Mud crab predation risk depended on predator treatment, as blue crabs consumed twice as many mud crabs as did toadfish, while only two crabs were cannibalized throughout all trials in the control mesocosms (Figure 6.2). The amount of time mud crabs spent hiding in refuge during the previous experiment also had a significant effect on predation risk (refuge use, estimate ± SE = –8.08 ± 3.99, t = –2.02, *P* = 0.0430) and strongly interacted with predator treatment (refuge use x predator treatment (blue crab versus toadfish), estimate ± SE = 10.07 ± 4.04, t = 2.50, *P* = 0.0126; Figure 6.3). Blue crabs preferentially consumed bold mud crabs with 87% of the crabs that exposed themselves ≥70% of the time lost to predation. By contrast, toadfish primarily selected shy crabs with only 9% of the crabs which exposed themselves ≥70% of the time consumed, and 0% of the crabs which exposed themselves ≥90% of the time (Figure 6.3). Additionally, half of the crabs consumed by blue crabs spent 30–70% of their time hiding in refuge, while half the crabs consumed by toadfish hid for 50–80% of the time (Figure 6.3). The distribution of mud crab personality types consumed by blue crabs and toadfish were thus considerably different (D = 0.64, *P* = 0.0233). Mud crab mortality was not significantly influenced by carapace width (size, estimate ± SE = –0.09 ± 0.06, t = –1.54, *P* = 0.1229) and did not substantially differ across trials (mean variance in mortality across treatments = 1.40).

Predator behavior

Blue crabs and toadfish exhibited drastically different amounts of time inside versus outside refuge (location, estimate ± SE = 1.52 ± 0.30, Z = 5.13, $P < 0.0001$) and moving versus stationary (mobility, estimate ± SE = 1.99 ± 0.31, Z = 6.34, $P < 0.0001$). Whereas blue crabs actively searched for prey, toadfish remained hidden within oyster clumps three times longer than blue crabs on average (Figure 6.4a). Observations of these predators also found that blue crabs were often mobile, spending five times longer than toadfish moving, whereas toadfish would remain still underneath the oysters (Figure 6.4b).

DISCUSSION

These findings support the conclusion that personality can help predict predation risk, and demonstrate that different personalities are best suited to distinct situations. Although mud crab refuge use and mortality were measured during two separate experiments, our previous research has determined that relative refuge use between individuals should remain consistent across these experiments (Griffen et al. 2012, Toscano et al. 2014b, Chapter 5). Crabs exhibited a wide range of behaviors along the continuum of bold versus shy personalities in the presence of both predators. However, the survival benefits of a particular personality varied as crabs displaying the same personality experienced different mortality rates depending on predator species encountered. Such results match conceptual predictions postulated by Sih et al. (2004, 2012) and Wolf & Weissing (2012) on the importance of personality for determining fitness and ecological processes.

Our observations on predator behavior confirm that blue crabs and toadfish use vastly different hunting strategies. Blue crab behavior was characteristic of active hunters, with crabs spending most of their time exposed outside of oyster clumps, and frequently moving about the enclosure. In comparison, toadfish behavior was representative of ambush predators, as the fish normally remained hidden and immobile underneath oysters. These behaviors are consistent with past observational studies which have investigated the foraging behavior of these predators (Price and Mensinger 1999, Hines 2007).

The consumption of specific personality types by predator species is probably a consequence of these differences in predator hunting mode. Bold mud crabs probably had higher mortality than shy crabs in the presence of blue crabs because they spent a substantial portion of their time outside oyster clumps in the same locations blue crabs frequented. Conversely, shy mud crabs most probably had elevated mortality in the presence of toadfish, because they remained under oyster clumps whereas toadfish tend to lie hidden in wait. While we did not examine the simultaneous occurrence of both blue crabs and toadfish in the presence of mud crabs, such circumstances will be rare and brief given the relatively low densities of these predators and their mobility. Mud crabs respond to both predators by hiding, so there should not be synergistic impacts on mud crab survival in these instances. In fact, toadfish may actually reduce predation by blue crabs by causing mud crabs to hide more frequently, and thus the simultaneous occurrence of these predators could have an overall positive impact on mud crab survival. The only other known study to examine the effects of prey personality in a multipredator system found that the personality type with the most successful escapes depended on predator species, but did not find personality to have as large an impact on prey survival (Blake and Gabor 2014). This may be because predators were not given a choice between prey personalities concurrently and had similar hunting strategies. The strong connection between predator and prey behavior illustrated here highlights the necessity of examining both simultaneously (discussed by Lima 2002).

Interestingly, although blue crabs and toadfish selected specific personality types, the personality these predators consumed were the least common personalities mud crabs displayed in the presence of that particular predator species. The strength of the mud crab predator avoidance behavior depended on predator species, with crabs increasing their refuge use in the presence of odor cues belonging to predators which cause the highest mortality (blue crabs). Other studies have described similar results with passerine birds and grasshoppers responding most strongly to owl and spider species which present the greatest predation threat (Morosinotto et al. 2010, Miller et al. 2014). However, our findings demonstrate that the strength of predator avoidance behaviors not only relies on predator hunting mode as previously theorized (Preisser et al. 2007, Miller et al. 2014), but also depends on prey personality. Here, personality comes into play when an individual has a disposition which naturally causes it to express the avoidance behavior and the predator consumes the opposite prey personality. Thus, predator avoidance behaviors should be the strongest when both the avoidance behavior and personality of the individual facilitate survival in the presence of a specific predator (e.g. prey will most often become inactive in the presence of predators which preferentially consume bolder individuals, and will be more active in the presence of predators which select shy individuals). Given the incredible variety of species which exhibit personalities and the numerous types of avoidance behaviors prey can exhibit in response to predators, these findings can be applied to a wide range of predator–prey interactions.

The link between personality type of prey and the suitability of that personality for the specific hunting mode of the predator could partially control the structure of communities. For example, the shift in mud crab refuge use in response to predator species reported here can govern trophic cascades. Previous research on *P. herbstii* established that the predator avoidance behavior involves a substantial decrease in crab foraging effort which has positive benefits for mussel survival (Grabowski 2004, Grabowski and Kimbro 2005, Grabowski et al. 2008, Griffen et al. 2012). Consequently, the presence of either blue crabs or toadfish probably controls the strength of this indirect interaction on bivalve mortality. Numerous studies have suggested that such non–consumptive effects of predators may be equivalent or greater than the consumptive effects as they propagate across trophic levels (Huang and Sih 1991, Wissinger and McGrady 1993, Peacor and Werner 2001, Preisser et al. 2005). Additionally, differences in the distribution of prey personalities within populations can have broad impacts on the community. Keiser and Pruitt (2009) determined that the personality composition of populations can be more important than population size in controlling overall foraging behavior, and Cote et al. (2011) found that personality composition affects offspring dispersal. Thus, by measuring the predation threat of different predators which is related to the strength of predator avoidance behaviors and their distribution within the population (Morosinotto et al. 2010, Miller et al. 2014, this study), ecologists could potentially estimate the relative impact of these behaviors on the community. Knowledge on the distribution of personalities within prey populations and the relative frequency of predator species with different hunting modes are therefore powerful tools that could be combined to determine the strength of predator–prey interactions in field settings, where prey commonly exhibit a wide variety of personalities and encounter multiple predator types.

Indeed, living in a multipredator system may explain why mud crabs generally increase their time underneath oysters to avoid predators. Numerous studies have documented mud crabs seeking refuge within oysters in response to toadfish (Grabowski and Kimbro 2005, Grabowski et al. 2008, Griffen et al. 2012, Toscano et al. 2014b, our behavioral data). Although the predator avoidance behavior is not as strong as with blue crabs, our results on mud crab mortality indicate that crabs should exhibit the opposite behavior when detecting toadfish (i.e. act boldly and leave oyster clumps). Crabs may therefore increase their time within refuge automatically when in the presence of a predator owing to the prevalence and heightened threat of predation from blue crabs. Mud crabs might also seek refuge in the presence of toadfish because of differences between crabs in experience or ability to distinguish predators. This further suggests that the maintenance of a variety of personalities in this system is driven by the simultaneous occurrence of different predator types. Our research demonstrates that the benefits of each personality type are context dependent where boldness is favored in the presence of toadfish and shyness in the presence of blue crabs. These personalities are thus likely to be sustained within the same population as both predators can be encountered within the system, and the lack of one personality would be disadvantageous if the wrong predator became prevalent in the environment. Such findings corroborate conceptual ecological theories on context dependent trait-performance (for a discussion on this concept, see Sih et al. 2004, Wolf and Weissing 2012).

Our results also reveal that different predators may shift the personality composition of prey populations to opposite extremes through two concurrent methods: by preferentially consuming specific personalities and by causing individuals to change their behavior (e.g. blue crabs consume bold mud crabs and cause individuals to hide more frequently, causing the population to shift towards shyness). Such shifts promoting a particular personality type could occur under a number of circumstances. Habitat destruction and fishing pressure often remove key predators from the system (Jennings and Polunin 1997, Wilcove et al. 1998), which can subsequently reduce the number of predators favoring a particular personality type (e.g. hypothetically, overfishing of blue crabs reduces the predation of bold mud crabs and need for individuals to act shyly, thus the population becomes bolder). Alternatively, the introduction of an invasive species could promote the supremacy of a particular prey personality if the introduced species displaces natural predators. In fact, invasive species are frequently associated with the decline of predator populations (Gurevitch and Padilla 2004), and numerous studies already demonstrate that alien species can alter the behavior of native species (for a brief list, see Strauss et al. 2006). Therefore, shifts in the distribution of personalities within populations is likely to be a common phenomenon, but has been rarely explored. Future studies should thus strive to incorporate the range of behaviors exhibited when investigating predator–prey interactions and personality researchers should more frequently report the distribution of personalities rather than just documenting that mean differences exist, as our findings demonstrate that these behaviors can have strong impacts which will not be resolved if only the average is used.

In conclusion, variations in prey personality and multiple predator species are both the norm rather than the exception in natural systems (Vilhunen and Hirvonen 2003, Sih et al. 2004, Preisser et al. 2007, Morosinotto et al. 2010, Sih et al. 2012, Wolf and Weissing 2012). The relationship between prey personality and predator hunting mode affects the survival and behavior of prey which has a large potential to control trophic cascades and acts as a mechanism for maintaining intraspecific trait variation. Insights into the personality composition of prey populations and hunting mode of predators may guide predictions on the strength of predator–prey interactions as well as the response of ecosystems to such pervasive issues as habitat destruction, overfishing and species invasions Therefore, the results of this study should be generally applicable to a wide variety of situations, and underscore the importance of behavioral traits in mediating predator–prey interactions.

ACKNOWLEDGMENTS

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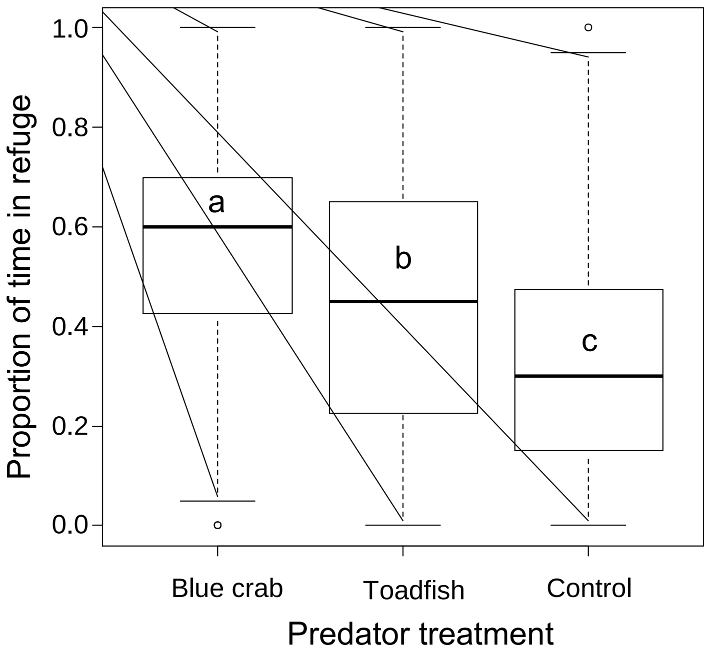

Figure 6.1 Proportion of time mud crabs, *Panopeus herbstii*, spent in refuge when exposed to different predator odour cues (blue crab *Callinectes sapidus*, toadfish *Opsanus tau*, and control of no cue; n ¼ 100). Boxes indicate the 25th and 75th percentiles; whiskers denote 1.5 x interquartile range and the median is shown by the horizontal line within each box. Data were grouped from 10 trials.

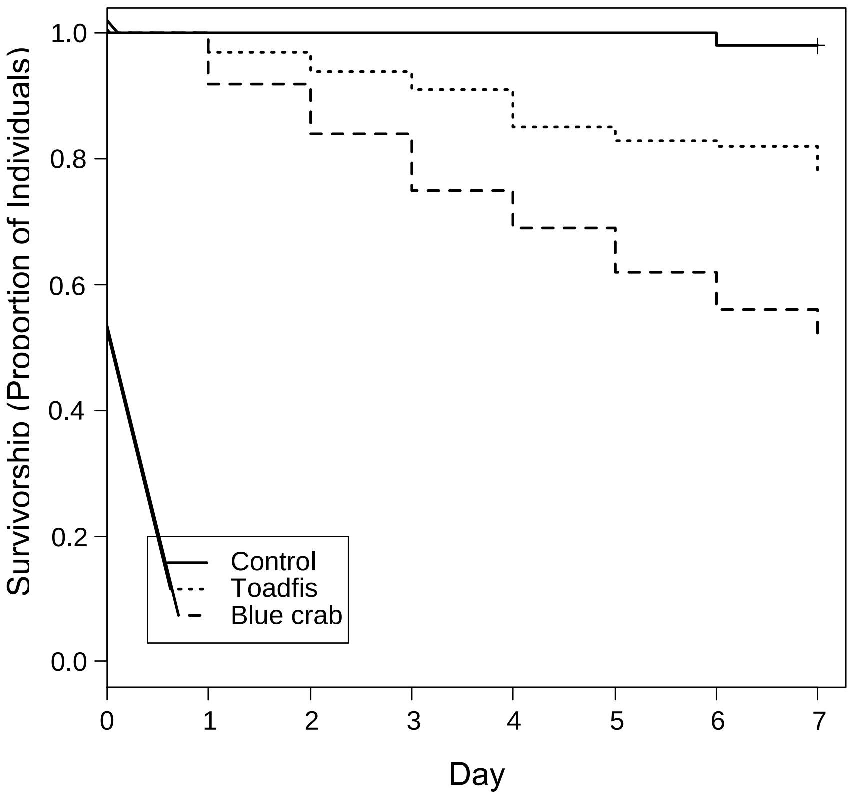

Figure 6.2 Survivorship curve of the proportion of individual mud crabs (*Panopeus herbstii*; n = 100) which survived each day as the experiment progressed. Lines denote mud crab exposure to different predators (blue crab, *Callinectes sapidus*; toadfish, *Opsanus tau*; and control of no predator).

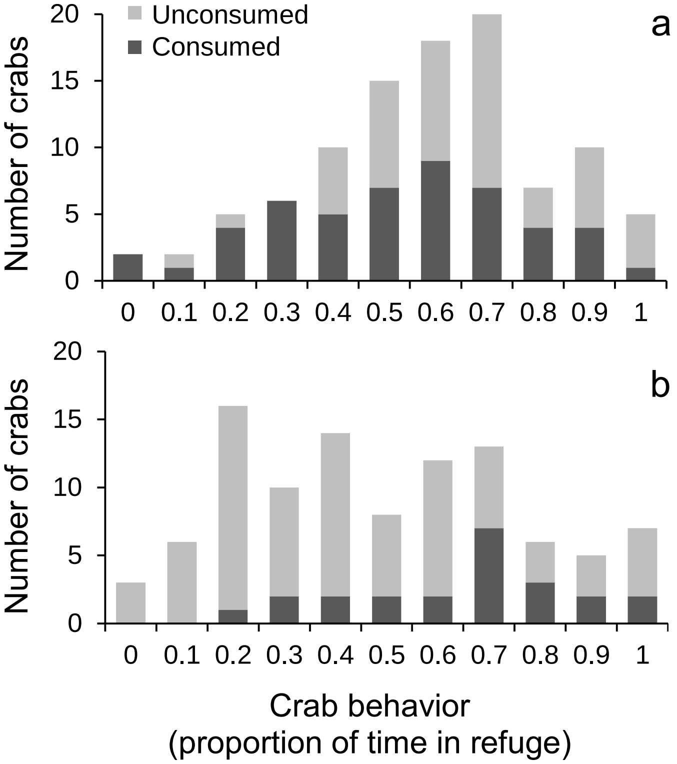

Figure 6.3 Histograms of the amount of mud crabs, *Panopeus herbstii*, consumed by predatory **(a)** blue crabs *Callinectes sapidus*, and **(b)** toadfish *Opsanus tau* for each behavioral class of mud crab. Crab behavior was measured as the proportion of observations over 3 h in which a crab was observed taking refuge under oyster shells.

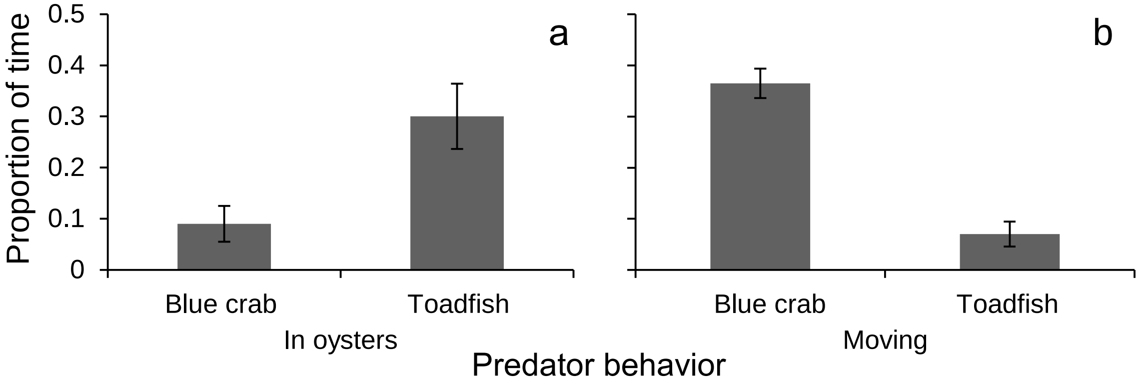

Figure 6.4 Mean ± SE proportion of time predatory blue crabs (*Callinectes sapidus*) and toadfish (*Opsanus tau*) **(a)** hid within oyster clumps and **(b)** were mobile. behavior was measured as the proportion of observations predators used cover within oysters and were moving over two 20 h periods which were measured on two separate days for a subset of the trials/individuals (n = 5).

CHAPTER 7

PERSONALITY INTERACTS WITH HABITAT QUALITY TO GOVERN INDIVIDUAL MORTALITY AND MIGRATION PATTERNS[6]

ABSTRACT

Animal personalities are increasingly recognized as key drivers of ecological processes. However, studies examining the relative importance of personalities in comparison to other environmental factors remain lacking. We performed two field experiments to assess the concurrent roles of personality and habitat quality in mediating individual mortality and migration. We quantified the predator avoidance response of mud crabs, *Panopeus herbstii*, collected from low and high quality oyster reefs and measured crab loss in a caging experiment. We simultaneously measured the distance crabs traveled as well as the stability of personalities across reef quality in a separate reciprocal transplant experiment. Habitat quality was the primary determinant of crab loss, although the distance crabs traveled was governed by personality which interacted with habitat quality to control the fate of crabs. While crabs on low quality reefs rapidly emigrated, starting with the boldest individuals, both bold and shy crabs would remain on high quality reefs for months and experienced higher predation risk, particularly among bold individuals. These findings suggest that personalities could produce vastly different

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population dynamics across habitat quality and govern community responses to habitat degradation.

INTRODUCTION

Individual mortality and migration rates are fundamental drivers of population and community dynamics as these life–history traits can influence such processes as gene flow, species' distribution, population growth, and inter/intraspecies encounter rates (Harwood and Hall 1990, McPeek and Peckarsky 1998, Clobert et al. 2001, Bowler and Benton 2005). Both mortality and migration are also common responses to environmental changes (e.g. habitat destruction, ocean acidification, seasonal change, climatic regime shifts). Understanding the factors which govern the mortality and migration responses to these global changes is therefore critical for managing populations and predicting the persistence of species in the face of these disturbances. One characteristic which has recently gained recognition as a crucial parameter within community interactions, and as a principle force in determining mortality and migration rates is animal personality (Cote et al. 2010, Dingemanse and Wolf 2010, Pennisi 2016).

Animal personalities, defined as consistent differences in individual behavior, have been documented across a broad range of phyla (Gosling 2001, Freeman and Gosling 2010, Stamps and Groothuis 2010), and have strong individual, population, and community level impacts (catalogued in Wolf and Weissing 2012). For instance, personalities can govern life history traits and fitness through differential use of the local environment (Both et al. 2005, Stamps 2007, Dingemanse et al. 2003). Additionally, personalities can shape community dynamics by cascading effects derived from distinctive species interactions (Griffen et al. 2012, Chapter 6) as well as through differential dispersal patterns (Cote and Clobert 2007) and disease spread (Krause et al. 2010). This behavioral variability has even been suggested to mediate invasion success (Carere and Gherardi 2013) and speciation (Wolf and Weissing 2012).

Despite widespread acknowledgement that animal personalities play an important role in community processes, our knowledge of the relative importance of personalities in comparison to other environmental parameters, such as habitat quality, remains limited. This is exacerbated by a dearth of field–based personality studies that span different contexts (Wolf and Weissing 2012, Dall and Griffith 2014). A number of studies have directly linked individual boldness and decreased refuge use to increased mortality (e.g. Bremner-Harrison et al. 2004, Chapter 6) and dispersal distance (e.g. Dingemanse et al. 2003, Cote et al. 2011). However, the opposite trend in mortality has also been found in some instances as the relationship can depend on the predator encountered (e.g. Réale and Festa-Bianchet 2003, Smith and Blumstein 2010). In turn, decreases in habitat quality have frequently been associated with elevated mortality (Rodwell et al. 2003, Cushman 2006), mass emigrations (Lenihan et al. 2001, Matter and Roland 2002) and altered movement patterns (Bélanger and Rodríguez 2002). Since habitat degradation commonly involves a loss in refuge availability, there is a high potential for interactions between personality and habitat quality to exist.

Nonetheless, our understanding of the potential interaction between personality and habitat quality is further constrained by the lack of empirical studies on the persistence of personalities (Cote et al. 2010). While personalities were traditionally viewed as stable and behaviorally limiting, recent theory suggests individuals can show considerable behavioral plasticity across contexts and may alter their behavior in response to dramatic changes in environmental conditions (i.e. behavioral reaction norms; Dingemanse et al. 2010, Dingemanse and Wolf 2013). Here, we conduct two field experiments to examine the interactive roles that personality and habitat quality play in governing individual mortality, migration, and behavioral stability within a model study system.

METHODS

Study system

We experimented in a spatially heterogeneous coastal habitat. Found worldwide, oyster reefs can be a dominant commercial and ecological component of estuaries, but have declined by 85% globally (Beck et al. 2011) due to a variety of anthropogenic sources including harvesting, sedimentation, disease, introduced pests, and oxygen depletion (Lenihan and Peterson 1998). The degradation of oyster reefs produces a gradient of high to low quality habitat, and has ramifications beyond the oysters themselves, as these organisms are considered ecosystem engineers that provide valuable shelter and food for a diverse array of species (Lenihan and Peterson 1998, Lenihan et al. 2001).

One such species is the mud crab, *Panopeus herbstii*, which is a common consumer within reefs along the Atlantic and Gulf coasts of the United States (McDonald 1982, Grabowski 2004). The mud crab is relatively stationary compared to other crab species which use the same habitat, as individual mud crabs can stay on the same reef for months (Toscano et al. 2014b), although some may travel >5 m over two days (Stachowicz and Hay 1999). Crab movement is primarily attributed to foraging upon bivalves such as juvenile oysters, *Crassostrea virginica*, and the scorched mussel

Brachidontes exustus (Toscano and Griffen 2012). However, crab movement can also comprise mate searching and brief competitive interactions (Belgrad, personal observations). Individuals greatly reduce their activity levels and increase their time in refuge in the presence of predators (Hughes et al. 2014), exhibiting a continuum of bold–shy personalities. Previous work in our laboratory has established that differences in this behavior between individuals can last for months (Toscano et al. 2014b), are correlated with individual energetic strategies (Toscano and Monaco 2015), and are consistent across a range of conditions, including predator presence/absence (Griffen et al. 2012), conspecific density changes (Chapter 5), and starvation levels (B.A. Belgrad 2015, unpublished data).

We conducted our study during the peak and mid spawning season of crabs on oyster reefs within the North Inlet National Estuarine Research Reserve in South Carolina (McDonald 1982). This estuary supports a mixture of low and high quality reefs that cover extensive areas within intertidal channels.

Effects of personality and reef quality on predation risk

We conducted a two-week caging experiment once during May and again during July, 2016 to determine how personality and habitat quality simultaneously govern individual mortality and movement in the field. Four low quality and four high quality reefs were sampled within North Inlet. Reef quality was determined by reef height since oyster survival and food availability strongly correlate with this parameter (Lenihan and Peterson 1998, Griffen and Norelli 2015). Low quality reefs were defined as reefs with heights less than 10 cm while high quality reefs had heights greater than 20 cm. Reef height was calculated following procedures described in Griffen and Norelli (2015).

Within each reef, we set up three haphazardly placed 2.5 m^2 plots that were spaced at least 5 m apart. A vexar mesh cage (pore size = 3.2 cm, height = 1.0 m) completely enclosed one plot to exclude predators, but allowed crabs to move freely out of the cage. Rebar (width = 1.9 cm, length = 2 m) and tent stakes (Coleman, length = 25.4 cm) were arrayed around the cage perimeter to keep the mesh edges buried ~3 cm into the sediment. No predatory toadfish, stone crabs, or blue crabs were found to have invaded the cages while sampling. The second plot only had two opposite sides staked with vexar mesh to control for the effects of caging. The final plot did not have any mesh to maintain natural reef conditions. Ten mature mud crabs (mean ± SD carapace width = 25.1 ± 1.9 mm; 204 males, 276 females) were collected by hand from each plot. Cohorts collected from the same plot were kept together throughout the entire study. Crab collections were blocked in time with two high and two low quality reefs sampled on one day and the remaining four reefs sampled the next day (n = 4 reefs of each quality). Collected crabs were brought to the Baruch Institute wet lab to assess individual personality.

Personality was assayed in natural cohorts following the protocol previously established in our lab (for a detailed description see Chapter 6). Briefly, cohorts were starved for 24 h to standardize hunger levels and placed inside separate flow–through mesocosms (circular with diameter 1 m; water height 15 cm). Crabs from both high–quality and low–quality reefs were subjected to a common garden experiment where individuals were exposed to oyster clumps of intermediate quality, relative to our field–sampled reefs, with ample structure to provide refuge, and with predator and prey odor cues delivered continuously. We conducted all observations at night under red light to ensure mud crabs were at their most active and were undisturbed by the observer. Crabs were given 10 min to acclimate once cohorts were placed in the mesocosms. After acclimating, we recorded whether each individually–marked crab was exposed on the shell surface layer or hiding underneath the oysters every 9 min for 3 h (20 observations for each crab). Refuge use was measured as the proportion of these 20 observations in which crabs were in refuge and not visible to the observer in the same manner used in prior studies of mud crab behavior (Griffen et al. 2012, Toscano et al. 2014b, Chapter 4, Chapter 5, Chapter 6).

Following behavioral observations, crabs were marked with individually numbered bee tags (the Bee Works, Orillia, Ontario, Canada) and released to the same plot from which they were collected. Every 48 h for two weeks each plot was exhaustively surveyed by hand during low tide to determine which individuals remained in the plots. Individuals not found within the completely enclosed plots were assumed to have emigrated from the region while those not found in the open plots may have either emigrated or been consumed by predators. Following the two week survey period, new plots were established in different sections of each reef and the experiment was repeated 1.5 months later to assess the consistency of our findings.

We evaluated how time to crab disappearance from plots was influenced by the fixed effects of caging treatment, reef quality, crab refuge use (i.e. personality measured in the lab), carapace width, gender and month sampled using a mixed–effects Cox proportional hazards model (i.e. a survival analysis). Reef ID and day collected were treated as random effects to control for repeated measures on the same reef and variables associated with sampling time (R package: *frailtyHL*). A Cox proportional hazards analysis is a statistical model which distinguishes between maximum values that represents a specific event occurring and those that simply represent the end of the observational period, then ranks the data accordingly (i.e. the data are right censored). This model therefore allowed us to right censor the data to account for crabs that were still found in our plots on the last day of the survey. This and all other analyses were conducted using R v3.2.3 (R Foundation for Statistical Computing, Vienna, Austria).

Effects of reef quality on migration

We simultaneously conducted a reciprocal transplant experiment between May and August 2016 to evaluate the roles that individual personality and habitat quality play in governing crab migration over extended timeframes under natural conditions. An additional six high–quality and six low–quality reefs were identified in the inlet. Three high and three low–quality reefs were randomly designated as transplant reefs while the remaining six reefs were controls. Twenty mature crabs (mean ± SD carapace width = 24.8 ± 1.8 mm; 135 males, 105 females) were collected from each reef. Crabs were collected by hand in cohorts of 10 individuals from 1 m^2 plots (two cohorts per reef). Sampling area was widened if 10 crabs were not found within the plots in an effort to maintain crab densities during behavior measurements and ensure each treatment had an equal number of crabs. Collections were blocked through time as each consecutive day one high and one low quality reef were sampled. We transported the crabs to the Baruch lab where their individual personality was assayed in the same manner as the previous experiment.

Within 24 h of quantifying personality, crabs were marked with numbered aluminum tags (diameter = 12.7 mm; The Tag Place). Crabs collected from transplant reefs were returned to reefs of the opposite quality while crabs collected from control reefs were returned to their original reefs. Numbered stakes were placed where crabs were released on each reef. Seven, 45, and 90 days after crabs were released, reefs were surveyed at low tide in a 25 m radius from the release points with a metal detector (Tesoro Sand Shark) and by hand to recapture crabs. Distance migrated from the stakes was measured during each survey. Crabs located at the day 7 survey were left undisturbed, while crabs found 45 and 90 days after their release were brought back to the lab and had their personality reassessed in the same manner as before to determine the extent that their personality changed over time. As not all crabs were recaptured for the behavior assay, supplementary crabs were caught from the same reefs to ensure that behavior continued to be measured in cohorts of 10. Crabs were again released 24 h after measuring behavior to either their transplant or control reefs depending on their treatment.

Given the large number of crabs that were not recaptured, recapture success and duration on reefs were analyzed with zero–inflated mixed–effects generalized linear models using a binomial and poisson distribution, respectively (GLMs; R package: *glmmADMB*). We treated transplant treatment, reef quality, crab refuge use, carapace width, and gender as fixed effects, and reef ID as well as day collected as random effects. Both the maximum distance crabs migrated and the distance traveled in the first week were analyzed with standard mixed–effects GLMs in the same manner as above (R package: *lme4*). We were unable to statistically analyze crab behavior changes due to vastly uneven recapture success across treatments. We discuss the trends in this data below.

RESULTS

Effects of personality and reef quality on predation risk

Reef quality had a significant influence on whether crabs remained in their plots during the caging experiment (estimate = –0.94, Z = –1.99, *P* = 0.047). Low quality plots had 44% more crabs disappear within 48 h than high quality plots, and no crabs remained in low quality plots throughout the entire experiment while 15 crabs stayed in high quality plots the entire time (Figure 7.1). Larger crabs also were found on plots significantly longer than small crabs even though the parameter effect size was small (Figure 7.2; estimate = 0.06, Z = 2.99, *P* = 0.003).

Although the main effects of caging treatment and personality were not found to be significant (estimate = –0.55, Z = –1.78, *P* = 0.076; estimate = 0.24, Z = 0.91, *P* = 0.363 respectively), both had significant two–way interactions with reef quality (estimate = 1.80, Z = 2.94, *P* = 0.003; estimate = –1.77, Z = –2.95, *P* = 0.003). The two–way interaction between caging treatment and reef quality likely arose because on low–quality reefs double the crabs were found at least once in completely enclosed plots compared to the partially caged and open plots (Figure 7.1a,c,e), whereas on high–quality reefs only ~56% more crabs were found in completely enclosed plots than in the other two treatments (Figure 7.1b,d,f). Crab personality and reef quality probably interacted because bolder individuals were found on low–quality reefs for shorter periods than on high–quality reefs. While bold crabs (exposed 70 – 100% of the time) on average were found in low–quality reef plots for less than 1/12 of the time observed in high–quality reefs, moderate crabs (exposed 45 – 65% of the time) were found within low–quality plots for ~1/7 of the time, and shy crabs (exposed 0 – 40% of the time) as much as 1/3 of the time observed within high–quality reefs. The increased recapture success of bold crabs on high–quality reefs was particularly notable in the completely enclosed cage treatment with crabs found almost twice as long on average in these plots (Fig. 1b) as in the partially caged (Figure 7.1d) and open plots (Figure 7.1f). Additionally, while all crabs were found in completely enclosed plots the longest for both high– and low–quality reefs, only in high quality reefs were bold crabs found more often in the plots than shy or moderate crabs. Consequently, there was a significant three–way interaction between crab personality, caging treatment, and reef quality (estimate = –3.85, Z = –3.40, *P* = 0.001). Neither month sampled nor gender had a significant impact on whether crabs were found (estimate = –0.01, Z = –0.02, *P* = 0.982; estimate = 0.02, Z = 0.29, *P* = 0.770).

Effects of personality and reef quality on migration

Many crabs did not remain on the same reefs long during the transplant experiment as only 61 out of 240 crabs were found seven days after their release, which dropped to 25 and 10 individuals 45 and 90 days after their release. This was acutely apparent on low–quality reefs since no crabs were found within those sampling sites after three months (Figure 7.3a,c). Significantly more crabs were recaptured when they were released within their original reef rather than when transplanted to a reef of the opposite quality, regardless of the quality of their original reef (estimate = 1.57, Z = 2.68, *P* = 0.008). On average, ~2.5 times more crabs were recaptured on high–quality than low–quality reefs (Figure 7.4). Although the main effects of crab personality and reef quality were insignificant (estimate = 0.02, Z = 0.02, *P* = 0.983; estimate = 0.13, Z = 0.16, *P* = 0.869 respectively), there was a significant three–way interaction between personality, reef quality, and transplant treatment (estimate = 2.44, Z = 3.37, *P* = 0.001). This interaction is likely a product of some moderate, and bold crabs remaining on high–quality reefs for at least 90 days (Figure 7.3b,d), while only a few shy individuals were found on low quality reefs 45 days after their release. (Figure 7.3a,c).

Crabs which did remain on the reef often did not travel far, as most individuals were found within three meters of their release point, and some within half a meter (Figure 7.5). Crab personality had a significant influence on individual migration distance (estimate = 0.12, Z = 2.72, $P = 0.007$). Bold crabs traveled farther than shy crabs, especially as time passed, since recaptured shy crabs on average remained within three meters for the entire study whereas recaptured bold crabs more than doubled this distance (Figure 7.5). These differences in distances are conservative since bold crabs were also 10% more likely to leave the sampling area later in the season. There was a significant two–way interaction between personality and transplant treatment as crabs on their original reef increased their migration distance with boldness while this trend was less pronounced in transplanted crabs because shy crabs would travel farther than their non–transplanted counterparts (estimate = 0.35, Z = 3.02, $P = 0.003$). A similar significant two–way interaction was seen between personality and reef quality as crabs on low–quality reefs had a strong positive relationship between crab boldness and distance traveled whereas this relationship was weaker on high–quality reefs (estimate = 1.06, Z = 14.42, $P < 0.001$). Consequently, there was a significant three–way interaction between personality, transplant treatment, and reef quality (estimate = –0.53, Z = –3.94, $P < 0.001$). Additionally, female crabs on average traveled 71% farther than males (estimate = 0.47, Z = 27.70, $P < 0.001$), and larger crabs traveled substantially farther than smaller individuals (Figure 7.6; estimate = 0.15, Z = 29.49, $P < 0.001$).

Finally, there were trends in behavioral changes among recaptured crabs, but this was not examined statistically because of the low number of crabs recaptured and the unequal sample sizes. While crabs which remained on their original reef did not display any major behavioral changes, regardless of reef quality, crabs transplanted to new reefs exhibited divergent behavioral alterations. Whereas crabs transplanted to low–quality reefs slightly decreased in boldness, crabs transplanted to high–quality reefs increased the proportion of time spent active by 67%.

DISCUSSION

We have demonstrated that personality interacts with habitat quality and can help predict predation risk and individual movement within the wild. Although habitat quality was the main predictor of crab recapture success, our data indicate that individual personality produces vastly different outcomes in each habitat type. Whereas high quality reefs were characterized by both bold and shy crabs remaining on the reefs for extended periods of time and moderate predation of bold individuals, our results suggest that low quality reefs had minimum levels of predation with the vast majority of crabs emigrating from the region immediately, starting with the boldest individuals. These results have important implications for numerous study systems and support conceptual theories on the role of personality in mediating community dynamics (Cote et al. 2010, Sih et al. 2012, Wolf and Weissing 2012, Spiegel et al. 2017).

Our conclusions are derived by the similarities in crab loss rates between the completely caged and partially caged/open plots which suggest that the majority of crab loss is from emigration out of the plots while the differences between treatments denote that predation risk is highest among bold individuals. Such findings are consistent with our previous laboratory predation study which found that bold crabs experience higher mortality (Chapter 6), and are further supported by the distances crabs traveled in the transplant experiment. Crabs which we were unable to locate on low quality reefs during the transplant experiment were predominantly assumed to have migrated out of the search area given the low predation rates estimated on low quality reefs inferred from the caging experiment. While some individuals may have simply been missed during sampling by burrowing below the limit of the metal detector, these cases were likely rare, as we also thoroughly sampled the regions by hand. Disturbance from resampling the reefs may have increased the likelihood of crabs emigrating from the region. However, even when our disturbance was the most frequent, crabs could regularly be discovered under the exact same oyster clumps they utilized previously. Contrary to a previous study on the same system using laboratory mesocosms (Grabowski 2004), crab mortality was highest in high–quality reefs. This observed increase in crab predation among high quality reefs likely stems from substantially more predators utilizing high quality rather than low quality reefs (Peterson 2003), and highlights the necessity of conducting field experiments.

Similar to many other field studies on habitat quality (Lenihan et al. 2001, Lin and Batzli 2001, Matter and Roland 2002, Rodwell 2003, Cushman 2006), we found that most individuals disappeared from low–quality habitat. Notably, crabs from different quality reefs faced different fates depending on their size and personality. Large crabs on low–quality reefs likely were found within plots longer than smaller crabs because their increased size helped protect them from predation, whereas this phenomenon was almost nonexistent on high quality reefs due to the abundance of oyster shell refuges which could hide smaller individuals (Figure 7.2). Additionally, bold crabs from low–quality reefs typically left the region within a week and generally traveled farther than their counterparts on high–quality reefs, whereas a few shy crabs remained for over a month. In contrast, bold crabs from high–quality reefs seemed to have higher levels of predation, and individuals stayed on the reefs for several months regardless of personality type. These results suggest that inhabitants of high–quality reefs are likely semi–permanent residents while most crabs found on low quality reefs are likely transients. This also suggests personality can cause individuals living within different quality habitats to exhibit distinctive community interactions. For example, the tendency of bold crabs to leave low–quality reefs and stay on high–quality reefs may encourage predators to follow the same pattern, as bold individuals seem to disproportionally feed upper trophic levels. In contrast, prey species on low quality reefs might inordinately benefit from having predominantly shy crabs remain on these reefs since *Panopeus herbstii* consumption rates correlate to boldness (Griffen et al. 2012, Toscano and Griffen 2014), and group personality composition has been found in some social species to be more important than group size in controlling foraging (Michelena et al. 2009, Keiser and Pruitt 2014).

At the population level, our findings suggest personality can influence the distribution of individuals by governing both migration distance and propensity to migrate. Indeed, bold crabs tended to migrate farther than shy crabs on both reef types and low–quality reefs commonly house a higher proportion of shy crabs than high–quality reefs (Chapter 4, this study). Such results substantiate personality–dependent simulations on the home range and distribution of individuals developed by Spiegel et al. (2017). Furthermore, the increased propensity of crabs to migrate on low–quality reefs corroborate migration models incorporating habitat quality (Taylor and Norris 2007), and our study shows that the addition of personality can help explain instances of partial migration within populations. Comparable relationships between boldness and migration have also been seen in fish (Fraser et al. 2001, Cote et al. 2011), birds (Dingemanse et al. 2003), lizards (Cote and Clobert 2007), and other crab species (Knotts and Griffen 2016), but none studied the simultaneous effects of habitat quality or mortality. Interestingly, even though the migratory behavior of bold crabs caused low–quality reefs to have greater proportions of shy crabs than high–quality reefs, increased predation pressure of bold crabs on high quality reefs can serve to dampen differences in personality distribution between reefs. Seasonal changes in predator density may therefore help explain fluctuations in the distribution of personalities that have previously been observed among individual reefs (Belgrad et al. 2017). Such considerations towards personality distributions are important because the personality composition of populations has been found to control population mating success (Sih and Watters 2005), offspring dispersal (Cote et al. 2011) and disease transmission (Keiser et al. 2016).

Our observations on the persistence of crab personalities indicate that the differences in community interactions discussed above between habitat types are relatively stable given that crabs which remained on their original reef maintained their personality for months. An observation seen previously in this system (Toscano et al. 2014b), but which had not been tested across different quality habitats. In fact, the behavioral changes in transplanted crabs suggest that these differences in community interactions may be magnified by habitat degradation and migration as bold individuals that migrate to high–quality reefs should become bolder while crabs that find themselves on degraded, low–quality reefs should either migrate or become shyer. These results provide mechanisms through which populations may develop spatially explicit personality structure. However, due to the low sample sizes from crab emigration, these findings remain tentative and should be researched further for statistical verification.

As variations in habitat quality become progressively more common from habitat fragmentation (Skole and Tucker 1993, Cushman 2006, Lindenmayer and Fischer 2013), harvesting of natural resources (Lenihan and Peterson 1998, Beck et al. 2011), and pollution (Fabricius 2005, Li et al. 2014), understanding how populations utilize spatially variable habitat will become increasingly important. The differences in mortality and migration that we have shown here demonstrate that population dynamics depend on personality and drastically differ across habitat quality. Furthermore, these personality–driven differences have a high potential to mediate divergent community interactions and trophic cascades. Evaluating the personality composition of populations may therefore be an effective metric for predicting community responses to habitat degradation.

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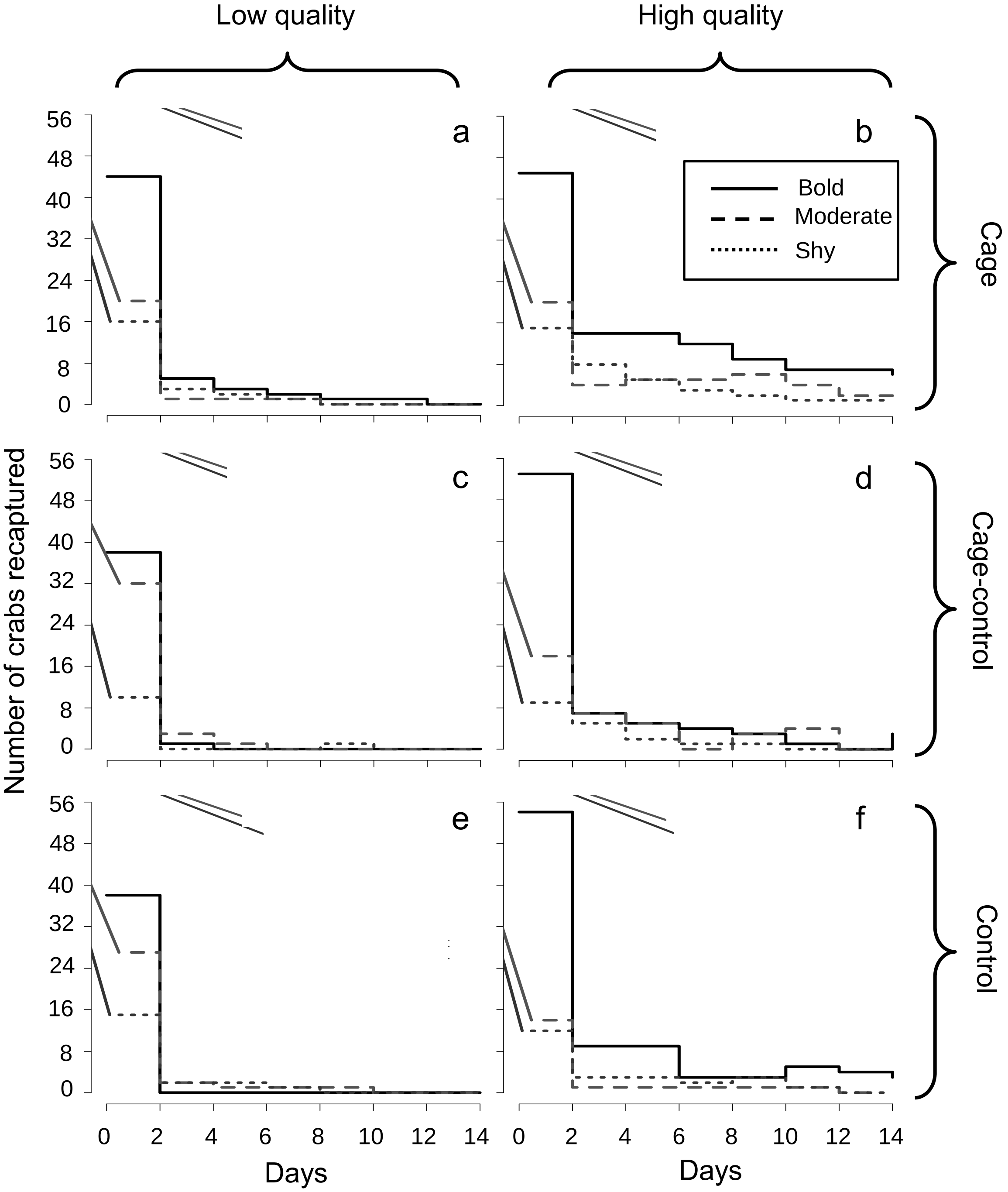

Figure 7.1 Number of bold (exposed 70 – 100% of time) moderate (45 – 65%) and shy crabs (0 – 40%) that remained within **(a,b)** completely enclosed, **(c,d)** partially enclosed, and **(e,f)** open 2.5 m^2 plots on **(a,c,e)** low quality and **(b,d,f)** high quality reefs over 14 days (n = 8 reefs total; 80 crabs per treatment). Day zero shows the initial personality distribution of crabs within each treatment. Increases in the step functions indicate crabs which left the plot one day and returned at a later sampling date.

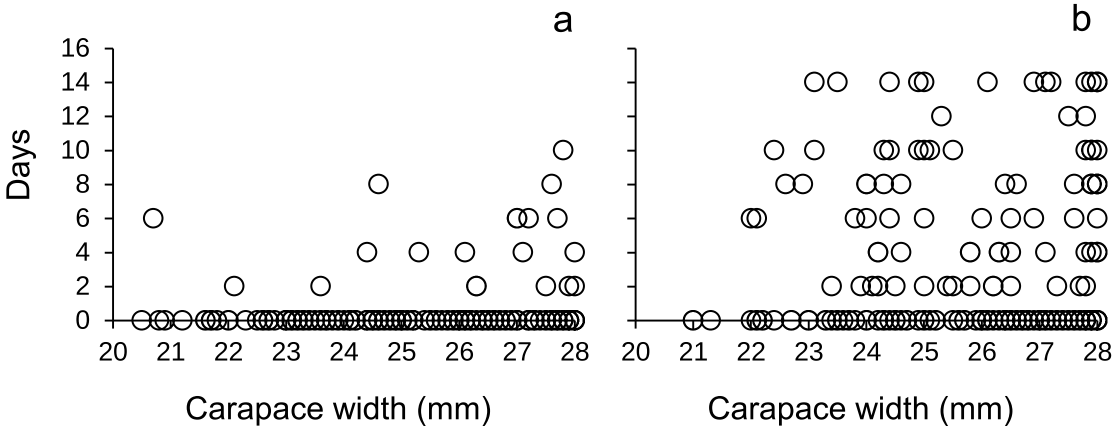

Figure 7.2 Number of days crabs were found within 2.5 m^2 plots within **(a)** low and **(b)** high quality reefs (n = 240 crabs per reef type).

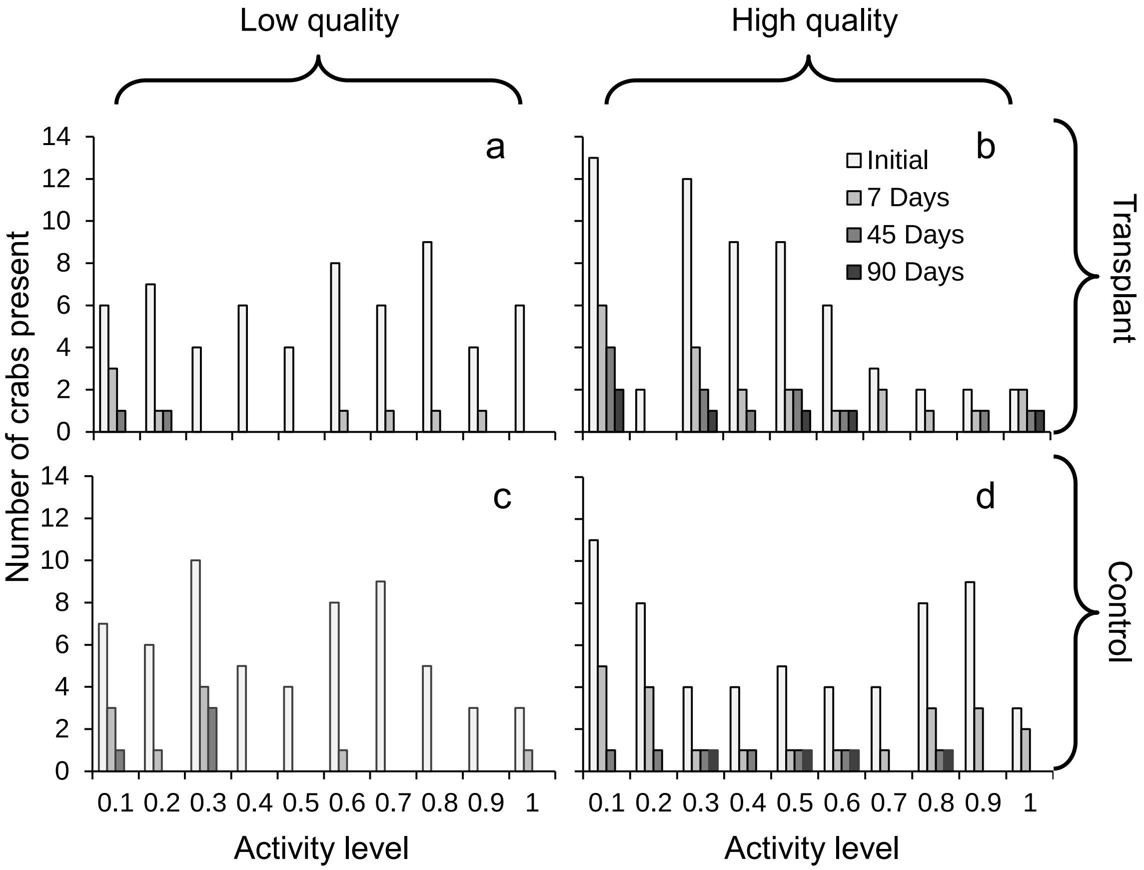

Figure 7.3 Number of crabs found within **(a,c)** low and **(b,d)** high quality reefs according to their initial activity level 7, 45, and 90 days after their release (n = 12 reefs total). Crabs were either **(a,b)** transplanted to reefs of the opposite quality or **(c,d)** originated on those reefs (control; n = 60 crabs per treatment). Activity level was measured as the proportion of time crabs spent active outside of refuge over 3 h.

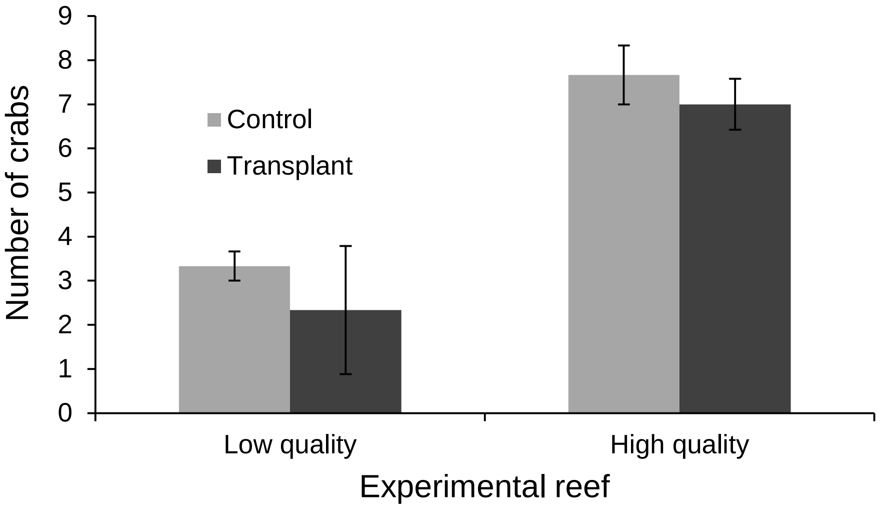

Figure 7.4 Mean ± SE number of crabs recaptured from low and high quality reefs (n = 12 reefs total) that were either transplanted to reefs of the opposite quality or originated on those reefs (control).

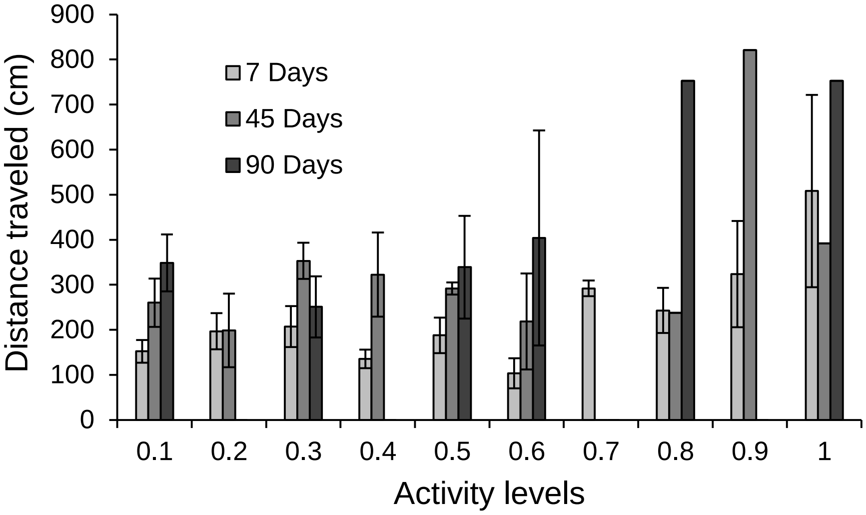

Figure 7.5 Mean ± SE distance crabs traveled (cm) from their release point according to their activity level (n = 1 – 16 depending on the category). Absence of error bars indicate that only one individual was captured in that category.

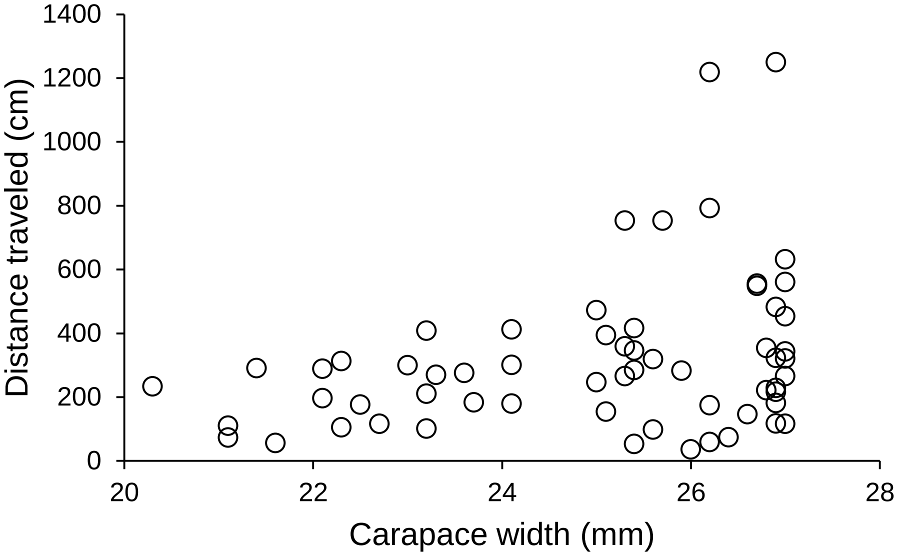

Figure 7.6 Relationship between crab carapace width (mm) and maximum distance traveled (cm) from their release point (n = 61).

CHAPTER 8

CONCLUSION

In an era of extraordinary global change in climate (Karl and Trenberth 2003, IPCC 2014), habitat quality (Travis 2003, Mantyka-pringle 2012), and species distribution/abundance (Lövei 1997, Estes et al. 2011), developing a mechanistic understanding of how the environment and internal forces shape ecological communities has become increasingly important for policy makers and stakeholders who benefit from ecosystem services. Species interactions play a central role in determining community structure (Wellborn et al. 1996), and are arguably one of the most complex components driving community dynamics. The strength of these interactions has been shown to depend on a number of variables ranging from the species in question (Peacor and Werner 2004) to the environmental context (Tylianakis et al. 2008) and time of year (Hu and Tessier 1995). A hallmark of these species interactions which exists in virtually every biological system is individual variation. However, only recently have scientists begun to explore the extent that individual differences control species interactions and community dynamics (Bolnick et al. 2011, Violle et al. 2012, Wolf and Weissing 2012). Thus, my dissertation examines how environmental forces produce individual phenotypic differences and the ensuing effect these differences can have on predator–prey interactions.

In my dissertation, I employ three common Brachyuran crab species to model the relationship between environmental variables (i.e. infection status, diet, habitat quality, season, and conspecific density), individual behavior, physiological condition, and mortality in the face of natural predators. This work demonstrates that individual phenotype heavily depends upon environmental conditions and interacts with the local habitat to control the fate of crabs in intertidal oyster reefs. For instance, crab energy stores were strongly influenced by diet and season (Chapters 3 and 4 respectively) while individual activity level and reproductive effort were subsequently linked to these energy stores and reef quality. Crabs captured from low quality reefs would generally be smaller, less active, and exhibit lower reproductive effort in comparison to crabs which occupied high quality reefs (Chapter 4). These results corroborate findings by Griffen and Norelli (2015), and also tie the effects of diet and reef quality to individual energy stores and behavior. Furthermore, crab activity level was sharply reduced by parasitic infection (Chapter 2) and decreases in conspecific density (Chapter 5).

Although individual crab behavior would change depending on the environmental context, I found that the relative differences in behavior between individuals remained reasonably similar across environmental gradients (e.g. active individuals would remain the most active individuals in the population even if the entire population became less active or vice versa; Chapter 5). This contributes to a growing list of literature establishing that behavioral differences among conspecifics are consistent across time and context, and that even behaviorally simple organisms exhibit personalities (Briffa et al. 2008, Griffen et al. 2012, Mowles et al. 2012, Kralj-Fišer and Schuett 2014, Toscano et al. 2014b, Seaman and Briffa 2015). Intriguingly, the behavioral plasticity of conspecifics was also found to vary and depended on individual personality (Chapter 5).

Such behavioral differences are important because they can govern how well individuals adapt to environmental changes (Wcislo 1989, Dingemanse et al. 2010).

Many of the environmental variables evaluated in my dissertation are frequently associated with each other in this and other systems. For example, reductions in habitat quality often coincide with a decrease in food availability/quality (Henley et al. 2000, Reichmuth et al. 2009, Griffen and Norelli 2015) and conspecific density (Heck Jr and Wetstone 1977, Cushman, 2006, Chapter 5) whereas seasonal changes can alter the prevalence of parasitic infection (Roy and Tandon 1992, Cosgrove et al. 2008, O'Shaughnessy et al. 2014). Interestingly, these environmental variables often create the same differences among individuals when they coincide in nature and therefore have a large potential to interact and compound their effects (e.g. low quality reefs and low conspecific densities are frequently associated with each other and both cause crabs to reduce their activity level). Since the effects of most of these environmental variables were measured independently of each other (e.g. parasitic infection, diet, conspecific density), many of my results are conservative estimates of phenotypic differences produced in the wild, particularly the observed behavioral differences.

In Chapter 6, I demonstrate that these differences between individuals cause members of the same population to have vastly different experiences and face different risks. Through a series of mesocosm experiments, I show that bold, more active crabs were generally consumed more often by predators than shy crabs, but that the survival benefits of a particular personality depended on the hunting mode of the predator species encountered. In the presence of an ambush predator, shy crabs would actually have higher mortality rates than bold individuals even though bold crabs would have the overall highest mortality rate upon encountering an active hunter. I also found that crabs would reduce their activity levels and increase their refuge use more in the presence of an active hunter than in the presence of an ambush predator. Such variations in predator–prey interaction strength are probably widespread given the prevalence of personality differences within populations (Gosling 2001, Sih et al. 2004) and the normalcy of living in a multipredator system (Vilhunen and Hirvonen 2003, Sih et al. 2004, Preisser et al. 2007, Sih et al. 2012).

In Chapter 7, I further demonstrate that individual differences in personality govern crab life-history traits. Here, personality is found to interact with habitat quality to mediate crab mortality and movement patterns in the wild. Unsurprisingly, bold crabs had higher mortality rates than shy crabs. Whereas both bold and shy crabs remained on high quality reefs for extended periods of time with modest predation of bold individuals, crabs on low quality reefs experienced minimal levels of predation, and instead, rapidly emigrated from the region starting with the boldest individuals. Unsurprisingly, bold crabs were also found to travel farther than shy crabs. This work sheds light onto the relative importance of personality for influencing community dynamics compared to other environmental factors, and provides rare field evidence of personality dependent mortality (Wolf and Weissing 2012, Dall and Griffith 2014).

The strong relationship between multiple physiological parameters, individual behavior, and survival documented in my research supports the newly popularized pace–of–life syndrome hypothesis (Réale et al. 2010). Scientists have recognized for decades that different species vary in their rate of reproduction, age at maturity, and longevity; and that most of these traits fall on a slow–fast continuum (i.e. low reproduction, slow development, long lifespans versus the opposite; Stearns 1992). The extremes of this continuum represent alternative strategies to maximize species fitness/success where trade–offs in resource investment cause these life–history traits to be correlated and preclude organisms from "adopting" the benefits of both strategies (e.g. high reproduction, fast development, large body size, long lifespan). Under these circumstances each strategy is best suited for a particular set of environmental conditions (e.g. stable versus extremely variable environment). Ricklefs and Wikelski (2002) extended this concept to include individuals in a population, and studies have begun to find links between physiological traits and life–history between populations (e.g. Wikelski et al. 2003, Tieleman et al. 2005, Závorka et al. 2015). However, behavioral traits have been conspicuously lacking from this framework (Biro and Stamps 2008, Réale et al. 2010). My research thus provides some of the first experimental evidence demonstrating that personality can be incorporated into this hypothesis.

My findings have several implications for population and community dynamics. Not only do I show that common environmental variables produce striking differences in physiological condition, reproductive output, and behavior, but also that these behavioral differences directly impact predation risk and movement patterns. At the population level, variation in crab reproductive effort and survival can regulate population growth rates. Additionally, personality differences may help govern the distribution of individuals since bold crabs have a higher propensity to migrate from low quality reefs and travel further than shy crabs (Spiegel et al. 2017, Chapter 7). This is supported by my reef surveys which found that high quality reefs house a higher proportion of bold crabs than low quality reefs (Chapter 4, Chapter 7). At the community level, phenotypic differences can impact upper trophic levels since crabs which are more fecund or bold are likely to disproportionally feed predators, either through their offspring (Steinhart et al. 2004) or by being consumed themselves (Chapter 6, Chapter 7). Personality differences can also affect lower trophic levels since more active crabs probably consume more prey. Indeed, previous studies in this system show that the behavioral differences found in my dissertation govern mussel consumption (Grabowski 2004, Toscano et al. 2014a) and mediate trophic cascades (Grabowski and Kimbro 2005, Grabowski et al. 2008, Griffen et al. 2012).

Overall, my research shows that phenotypic differences are tightly coupled to the environment and play a strong role in mediating community structure. The principles conveyed here can be applied to a diverse array of systems. The behavioral differences seen in my research have been recorded in an extensive variety of taxa (Gosling 2001, Sih et al. 2004, Biro and Stamps 2008, Wolf and Weissing 2012) and variation in parasite presence, diet, conspecific density, and habitat quality are widespread phenomena (Wilcove et al. 1998, Warren et al. 2001, Torchin et al. 2002, Bolnick et al. 2003, Travis 2003, Goode et al. 2005). Although individual differences in community dynamics have frequently either been ignored or considered too complex to incorporate in predictive frameworks (Bolnick et al. 2011, Violle et al. 2011), advances in computer technology and the advent of agent–based models makes this variability increasingly easy to include (Grimm and Railsback 2005). By accounting for individual phenotypic differences, scientists will be able to more effectively predict and manage community responses to such global threats as species invasions, overfishing, and habitat degradation.

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APPENDIX A

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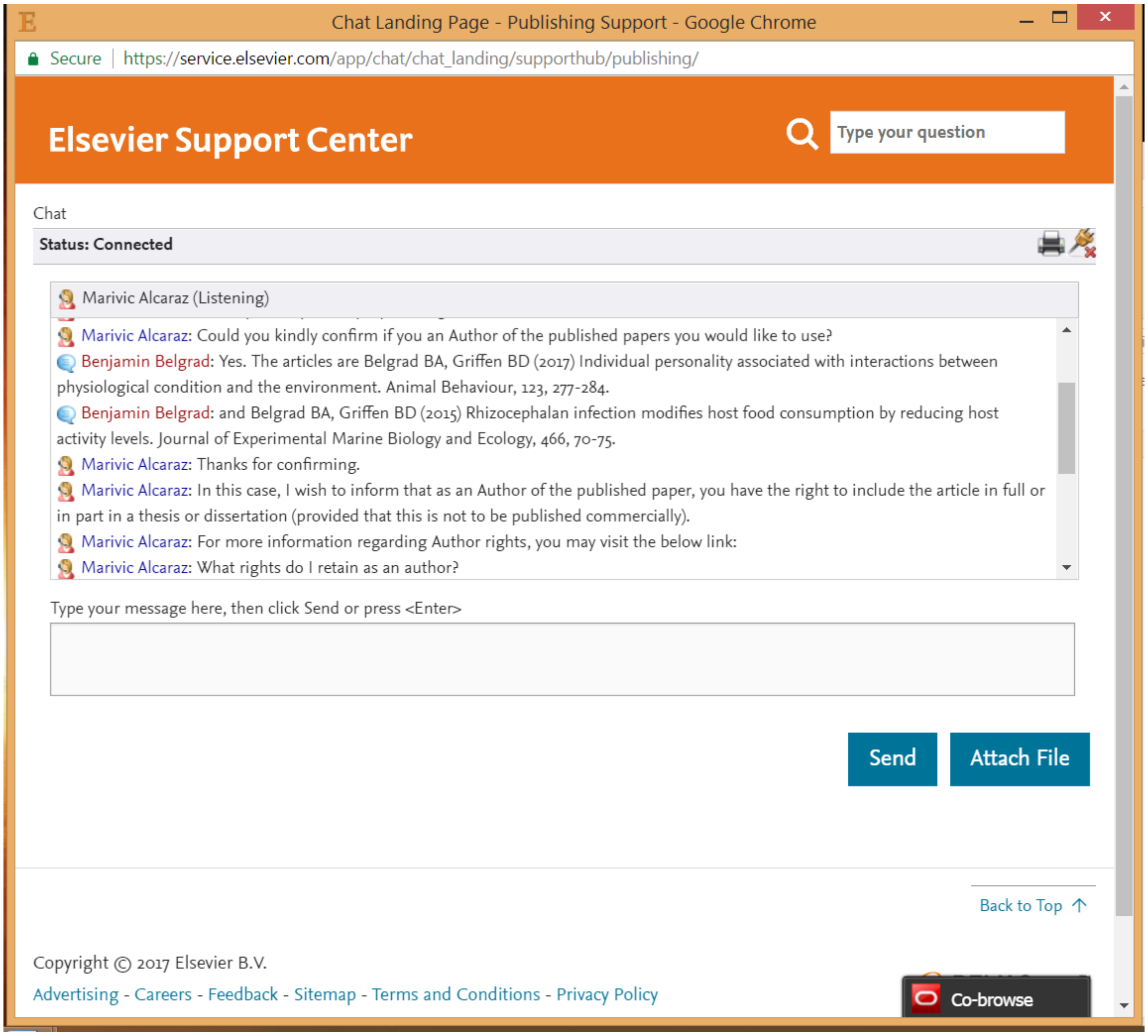

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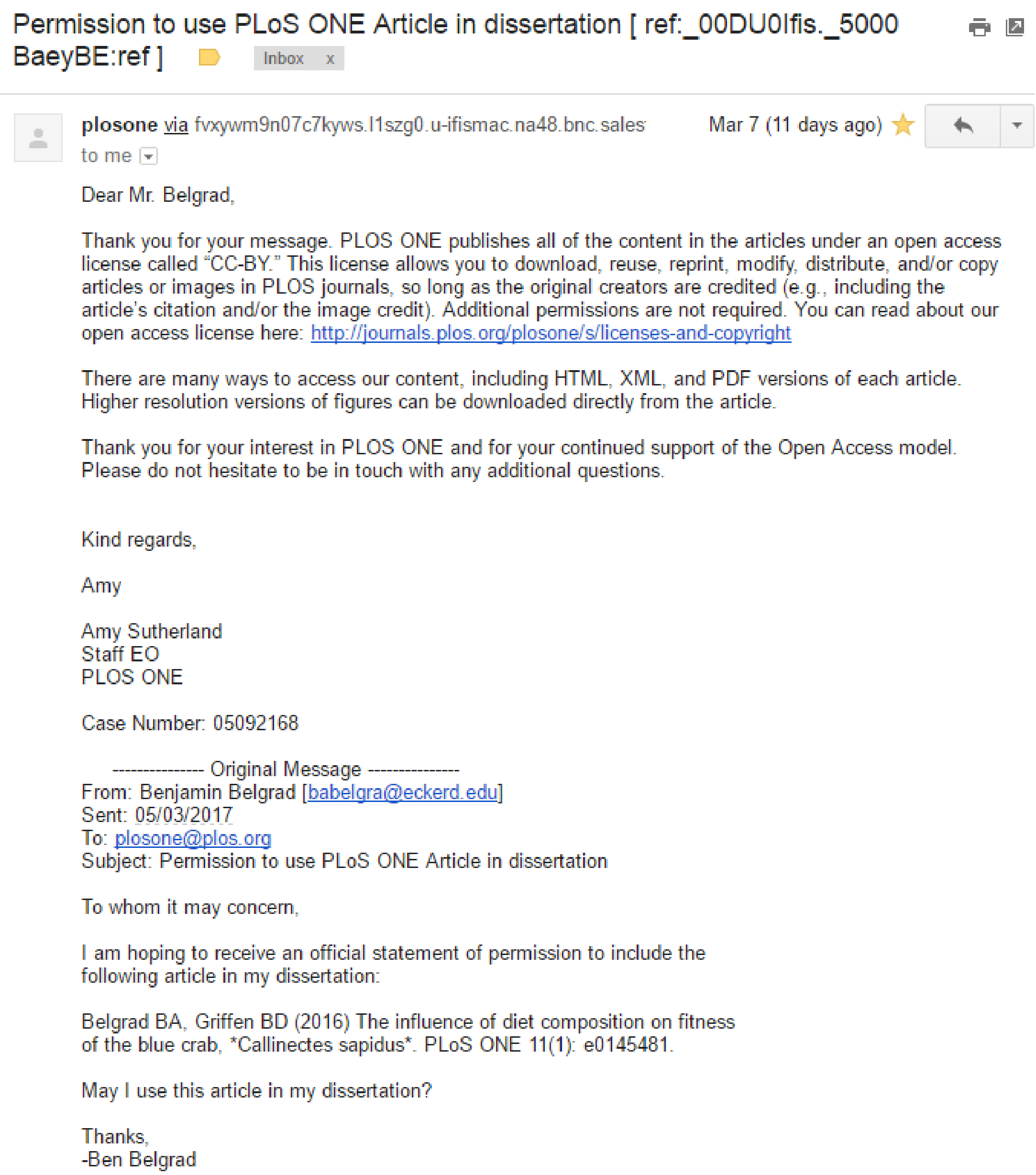

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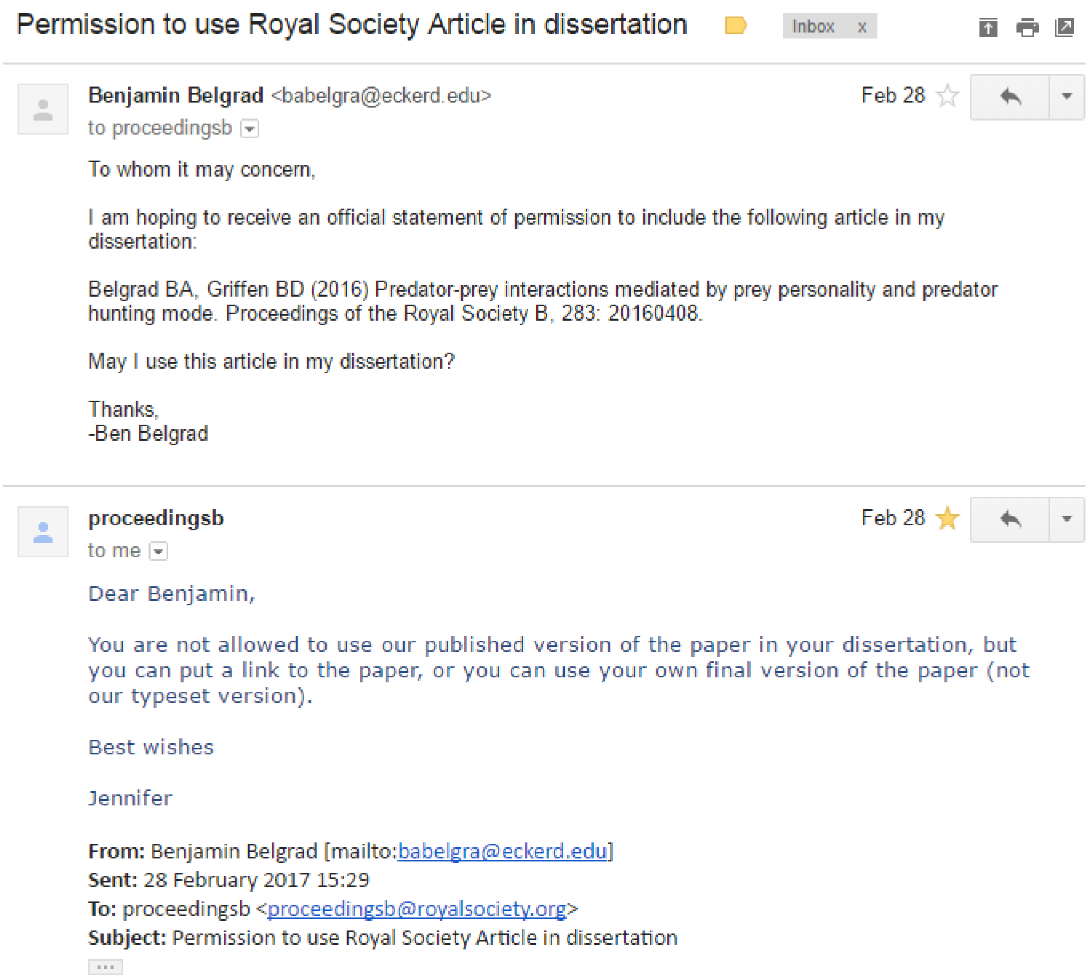

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