Underwater video as a tool to examine American lobster (*Homarus americanus*) trapping behaviour and interactions with invasive European green crab (*Carcinus maenas*).

By Nicola Zargarpour

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Abstract:

Species invasions pose a global threat to marine biodiversity, but their impacts can be complex and nonlinear. The European green crab (*Carcinus maenas*) is a marine invasive species present in nearshore waters of insular Newfoundland (NL). While the negative impact of green crab on eelgrass (*Zostera marina*) – a habitat-forming species – is well-understood, their direct impact on local fisheries is unclear. The collapse of American lobster (*Homarus americanus*) catch rates in green crab-invaded systems in Placentia Bay, NL led industry to suspect that the invasive species may be interfering with the ability of lobster traps to catch their target species. In this thesis, I examine whether green crab in and around lobster traps affect catch and retention rates of lobster using underwater video to observe traps as they fished. Our results from 2015 showed little co-occurrence between lobster and green crab in both catch and video data. However, this research provided the information necessary to design future quantitative studies involving the impact of invasive green crabs on the catchability of lobster, which we examined during a second field season in 2016. During this field study we conducted an *in situ* experiment in which we tethered green crabs in lobster traps, and assessed impacts on gear performance using scuba divers, underwater cameras, and by comparing catch rates of traps. Our primary finding was that crabs tethered in traps reduced lobster entry rates into the gear, but that the effect occurred both with invasive and native crabs.

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Chapter 1 - General Introduction

Species invasions pose a global threat to marine biodiversity (Carlton, 2000). In most cases the speed and magnitude of an invasion can exceed the resources available to achieve complete eradication (Van Driesche et al., 2008). Marine invaders cause a wide range of ecological effects including predation-mediated extinctions of naïve endemic species, as well as shifts in abundance and distribution of native species through competitive exclusion (Baxter et al., 2008; Gurevitch and Padilla, 2004; Molnar et al., 2008).

European green crab (*Carcinus maenas*, Linnaeus, 1758), which are native to Europe and Northern Africa (Williams, 1984), have invaded the nearshore marine ecosystems of every continent except Antarctica (Carlton and Cohen, 2003) and the species has been ranked among the 100 worst alien invasive species in the world (Lowe et al. 2000). Its wide tolerance for salinity, oxygen, temperature, and habitat type along with its high fecundity and propensity for omnivory make it an excellent invader (Klassen and Locke, 2007). Green crab occupy a wide range of habitats within sheltered areas of intertidal and estuarine zones (Ray, 2005). They are able to tolerate temperatures between 0 and 35 degrees Celsius and salinities ranging from 4 to 52‰ (Cohen et al., 1995) making them successful at adapting to changing climate regimes. Increasing sea temperatures as a result of human-mediated climate change can affect the growth and reproduction of marine invertebrates and fish as well as the habitats that they reside in (Brown et al. 2004; Côté and Green, 2012).

Green crab were first detected outside their native range in the early 19th century in north-eastern United States, likely transported via ballast or hull fouling (Behrens Yamada, 2001). During the years that followed, green crab populations moved northward, finally reaching the Canadian border in 1951, establishing in the Bay of Fundy and south-eastern Nova Scotia by the 1960s, and subsequently in north-eastern Nova Scotia by the 1990s (Carlton and Cohen, 2003). Research has suggested that northern populations of green crab originated from northern Europe as a result of a cryptic secondary introduction in the late 1980's by a more cold-tolerant population (Roman, 2006). As a result of two independent introductions of green crab from northern and southern European populations, there are two genetically distinct ecotypes (Jeffery et al., 2017). Tepolt and Somero, (2014) found that the temperature at which cardiac function fails in adult crabs is higher in southern populations as opposed to their northern, cold-adapted counterparts in both native and introduced ranges. They suggest that latitudinal patterns in thermal tolerance initially evolved in the native range, have since facilitated the spread of populations in eastern North America. Using genomewide climate-associated single nucleotide polymorphisms (SNPs) obtained by using restriction-site associated DNA sequencing (RAD-seq) of green crab in eastern North America, Jeffery et al., (2018) found that green crab genetic spatial structure was strongly influenced by winter sea surface temperatures. They suggest that the persistent spread of green crab in the Northwest Atlantic Ocean is limited by the minimum temperature each year, leading to reduced gene flow and range constraints of the two disparate green crab ecotypes. Importantly, warming sea surface temperatures, as a result of human-mediated climate change, could potentially influence the expansion and distribution of these ecotypes in Eastern North America.

Green crab inhabit both the rocky intertidal and subtidal zones, areas that also provide critical nursery habitat for early life stages of lobster (*Homarus americanus*) (Wahle and Steneck, 1992). Lobster may remain in nursery habitats for five years or more until they reach sexual maturity (Cooper and Uzmann, 1980). Sexually mature adult lobster are less vulnerable to predators and will spend time in unsheltered areas (Lawton and Lavalli, 1995). Green crab often occur in high densities and their diet shows considerable overlap with lobster (Elner, 1981; Lawton and Lavalli, 1995). In laboratory experiments, Rossong et al., (2006) demonstrated that adult green crab are capable of capturing and killing lobster up to 40 mm carapace length (CL). The complex interplay between predation, habitat availability, and size can influence lobster survival (Wahle, 2003).

Green crab are highly skilled consumers and can outcompete juvenile and sub-adult American lobster (*Homarus americanus,* H. Milne Edwards, 1837) for limited food resources and can actively prey on juvenile lobster in laboratory studies (Rossong et al. 2006; Williams et al. 2006). This could have implications for lobster recruitment and abundance given that field studies have identified the presence of green crab in areas with juvenile lobster habitats (Lynch and Rochette, 2009). Moreover, green crab can have an indirect effect on juvenile lobster behaviour. Laboratory studies suggest that in the presence of green crab, juvenile lobster spend less time foraging, more time in shelter and more time locating a food source (Rossong et al. 2011). Overall, the indirect effects of green crab on juvenile lobster behaviour could impact recruitment by lowering their energetic intake and exposing them to predation during a particularly vulnerable time in the early life stages of their benthic life cycle.

Importantly, studies have shown that green crab from different source populations can have varying ecological impacts on lobster (Haarr and Rochette, 2012). Given the agonistic interactions between green crab and lobster are complex and context dependent it is important to study the interactions within the invaded system itself and address mitigation strategies on a site-specific basis.

European green crab were discovered in North Harbour, Placentia Bay, Newfoundland in August 2007 (Klassen and Locke, 2007; McKenzie et al., 2011). However, demographic data and surveys suggest that populations were introduced and establishing in Placentia Bay in early 2000's (Blakeslee et al. 2010). Genetic data suggests that central/western Scotian Shelf populations, comprised of genotypes from introductions in both the 1800s and late 1980s, were the likely source for the anthropogenic introduction via domestic shipping (Blakeslee et al. 2010).

The lobster fishery is of great economic importance to the province of Newfoundland and Labrador as well as Canada, and in 2015 lobster landings were valued at $32 million (DFA, 2016). Within the Newfoundland lobster fishery, fishers have reported catching green crab in lobster traps. As a result, fishers have moved gear away from invaded areas to avoid the possibility of green crabs consuming the bait used in their traps (Fishermen's Voice, 2014). In one fisher survey, 89% of members of a fishermen's association in Guysborough County, Nova Scotia reported green crab in their lobster traps (JCG

Resource Consultants, 2002). The invasion could have wide reaching implications for lobster fisheries across Canada.

The ability of green crab to alter ecosystem dynamics makes them a serious potential threat to marine fisheries (Matheson et al., 2016). Lobster fishers have noted reduced catch rates as well as green crab in lobster traps in invaded areas (DFO, 2011). However, little is known about the mechanism by which this reduction could occur, making it challenging to implement responses within the fishery.

The interplay between behavioural, physiological and environmental factors can strongly influence the likelihood that a lobster will encounter, successfully enter and be captured by a trap. Before a lobster may attempt an entry, it must first find the trap. This can depend on the density of lobster in the surrounding area, the foraging area of individuals, as well as the density of traps in the water (Jernakoff and Phillips, 1988; Skajaa et al. 1998). Once a lobster is able to locate a trap, a number of factors can influence the chances that it will enter and be retained. These include the number of individuals already inside the trap (Addison, 1995), predator density, size (Jury and Watson, 2013), satiation, season, water temperature, sex, habitat type (Miller, 1990, 1980), as well as agonistic interactions inside and around the trap (Jury et al., 2001; Richards et al., 1983). Based on behavioural observations of lobster in and around traps deployed in the field, Jury et al. (2001) found that interactions between lobster attempting to enter the trap and those in the kitchen (entrance compartment) strongly limited the rate of lobster entry. If green crab and lobster commonly interact in traps, then green crab could be contributing to reductions in lobster catch rates

Previous studies have investigated how interspecific and intraspecific behaviours can influence lobster catch efficiency; these typically use catch data in combination with laboratory trials. There is a burgeoning body of work using underwater video to quantitatively assess trap capture efficiency from video observations *in situ* (Bergshoeff et al., 2018; Jury et al., 2001; Meintzer et al., 2017; Watson and Jury, 2013). This approach allows us to assess more nuanced effects of behavioural interactions on trap catch, beyond what we can glean merely from a count of individuals inside a trap at the end of a soak period.

The generalizability of results from laboratory-based studies can be questionable, particularly in complex ecosystems such as those invaded by the green crab. Therefore, in this study, we adopted a field-based approach, focused on filling a critical gap in knowledge with regard to understanding the interactions between green crab and lobster in nature, and how this could affect lobster capture efficiency within the fishery. Using underwater cameras attached to lobster traps we were able to observe these interactions *in situ*, obtaining critical information with regard to the nuanced behavioural aspects that contribute to lobster capture efficiency. In addition, we conducted SCUBA surveys using a procedure similar to Watson and Jury, (2013) to obtain estimates of the relative abundance of green crab and lobster in lobster fishing areas to assess the extent of overlap between these two species. We also incorporated trap pre-stocking techniques similar to those performed by Watson and Jury, (2013) to determine the influence of existing crabs, both native rock crab (*Cancer irroratus*) and invasive green crab on subsequent lobster trap entries. Overall, we used our catch data and concurrent video and SCUBA data to measure how green crab presence in and around lobster traps influenced the ability of those traps to catch their target species.

The main objectives of this thesis were to use trap video data to determine to what extent reduced catch rates are caused by inter/intra-specific aggression, bait depletion, competition for space or access to the trap. Additionally, we wanted to assess whether there was a reduction in lobster catch in relation to green crab ambient density observed via our SCUBA based surveys. In a broader context, the goal of this research is to help inform effective responses to mitigate the destabilizing impact that invasive species can have on the marine environment as well as fisheries that are reliant on them.

Co-authorship Statement:

The funding for this research was secured by Nicola Zargarpour, Dr. Brett Favaro, Dr. Cynthia McKenzie, and Kiley Best. The present study was designed by Nicola Zargarpour, Dr. Brett Favaro, Dr. Cynthia McKenzie, and Kiley Best. Nicola Zargarpour performed the fieldwork. Analysis was done by Nicola Zargarpour and Dr. Brett Favaro. Resources for fieldwork were contributed by Nicola Zargarpour, Dr. Brett Favaro, and Dr. Cynthia McKenzie. Dr. Brett Favaro, Dr. Cynthia McKenzie, and Kiley Best reviewed the thesis and provided comments. Academic mentorship was provided by Dr. Brett Favaro, Dr. Cynthia McKenzie, and Kiley Best

Chapter 2.

Evaluating the impact of invasive green crab (*Carcinus maenas*) on American lobster (*Homarus americanus*) catch efficiency using underwater video techniques.

1.1 Abstract

The European green crab (*Carcinus maenas*) is an invasive species recognized as having negative impacts on marine and estuarine biotic communities. First identified in Newfoundland waters in 2007, they have since spread across the south and west coasts of the island. Their ability to alter ecosystem dynamics makes them a serious potential threat to marine fisheries. Since the invasion began there have been anecdotal reports of green crab appearing in lobster traps. If green crab and lobster commonly interact in traps, then green crab could be contributing to reductions in lobster catch rates. The main objective for this study is to examine whether green crab interfere with the ability of lobster traps to catch American Lobster (*Homarus americanus*). To conduct this research, we designed and constructed custom underwater camera apparatuses capable of recording high definition video for 13 hour deployments. We attached these cameras to wire and wooden lobster traps, and deployed them in invaded locations across Newfoundland in the spring and summer of 2015 to investigate how green crab interact with each type of fishing gear *in situ.* We examined whether reduced catch rates are a result of green crab directly interfering with the lobster capture process through either depleting the bait, or impeding lobster entry. Our results showed little co-occurrence between lobster and green crab in both catch and video data; highlighting the need to better understand threshold levels for impact.

1.2 Introduction

Species invasions within marine ecosystems can drive ecological changes through direct and indirect effects, and can have wide reaching implications for fisheries. The conservation and management of marine resources requires that we understand the impact an invasive species can have on ecosystem dynamics. The European green crab (*Carcinus maenas*) is a crustacean species native to North African and European waters (Williams, 1984), and is considered to be among the 100 worst alien invasive species in the world (Lowe et al., 2000). It has invaded ecosystems across the globe, and was discovered in nearshore waters of Newfoundland in 2007 (DFO, 2011).

Green crab populations on the east coast of North America are thought to be made up of northern and southern genotypes as a result of two distinct introduction events. These originated from southern Europe in the early 1800's as well as from northern Europe in the late 1980's (Blakeslee et al., 2010; Roman, 2006).

Since 2007, green crab have spread across the south and west coasts of the island of Newfoundland. These populations are made up of both southern and northern genotypes and genetic analysis indicates a close match to the more cold-tolerant, northern populations (Blakeslee et al., 2010; Roman, 2006). This invasion is concerning because green crab destroy eelgrass beds (DFO, 2011; Matheson et al., 2016), are predators of clams and other bivalves (Klassen and Locke, 2007; Matheson and McKenzie, 2014), and compete with other crustaceans for habitat and food (Cohen et al., 1995). The impact of green crab on eelgrass beds are especially concerning because eelgrass habitat is extremely important for commercially important species such as cod, herring, shrimp and lobster, providing structured nursery habitat and refuge (DFO, 2009; Heck et al., 2003; Joseph et al., 2013; Short et al., 2006). Their ability to alter ecosystem dynamics make them a serious threat to many crustacean and bivalve fisheries (DFO, 2011).

Fish harvesters have raised concerns that the green crab invasion has already impacted the lobster fishery in Placentia Bay and other more recently invaded bays are vulnerable to this impact including Fortune Bay, which currently accounts for 40% of lobster landings across all active lobster fishing areas in the province (DFO, 2016a). Since the Newfoundland invasion began there have been anecdotal reports of green crabs appearing in lobster traps. If green crabs and lobsters commonly interact in traps, then green crabs could be contributing to reductions in lobster catch rates.

Interestingly, (Jeffery et al., 2018) suggest green crab populations on the west coast (St. George's Bay) are genetically distinct from those on the south east coast (Placentia Bay) and could, as a result, exhibit different behaviours and invasion characteristics. Further, green crab aggression and feeding behaviour has been shown to vary across sites (Rossong et al., 2012), and may therefore have the potential to influence catch rates and trap performance between fishing areas.

The American Lobster (*Homarus americanus*) is a decapod crustacean native to Newfoundland waters which make up the northern extent of the species distribution (Butler et al., 2006). In its northern range, lobsters can take between eight to ten years to reach the minimum legal size of >82.5 mm in carapace length (CL) (DFO, 2016a). Between the months of July and September, molting, mating, egg extrusion, and hatching occur (DFO, 2016a). Female lobster will extrude eggs roughly one year prior to mating and carry them in clutches for 9-12 months on the underside of their tail. From late May through to September hatching occurs, releasing the larvae which swim upwards and subsequently undergo three molts during their 4-6 week planktonic phase. After the third molt they settle to the benthic environment as newly developed postlarvae and will undergo further development before reaching sexual maturity. Commercial harvesting accounts for the majority of adult mortality, as adult lobster are thought to have few natural predators.

The lobster fishery in Newfoundland occurs during an 8-10 week period. Traps are deployed from small boats at depths usually less than 20 m. Licensing as well as daily trap limits (between 100-300, depending on the Lobster Fishing Area-LFA) are put in place by DFO to control fishing effort. As of 2016, there were around 2,450 licenses issued. Regulations also prohibit the harvest of undersized (<82.5 mm carapace length) as well as egg-bearing females, and all traps are required to have vents through which undersized lobster can escape. In addition, v-notching, whereby a shallow mark is made in the tail of an egg-bearing female is voluntarily practiced to ensure ovigerous females are not retained. The stock is currently assessed every three years based on indicators including reported landings, nominal effort (based on active fishers, fishing days, and trap limits), mean catch per unit effort (CPUE), and relative survival fraction (the fractional difference in predicted ratio at the beginning and end of the fishing season) for each of four regions (Northeast, Avalon, South Coast and West Coast) (DFO, 2016a). The assessment is based on fishery-dependent data only and does not account for local sales, handling mortalities and poaching that can occur before the catch is sold.

Within the Avalon region, LFA 10 which includes Placentia Bay and other areas of the Avalon Pennisula) reported landings have declined from 427 tonnes in 1992 to 20 tonnes in 2017 (DFO, 2018). For the South Coast region (LFA11, corresponding to Fortune Bay) reported landings have increased from 500 tonnes in 1992 to 1078 tonnes in 2015 (DFO, 2018). Finally, for the west coast region (LFA 13-14, corresponding to St. George's Bay, Bonne Bay and Penguin Arm in our study) reported landings have varied without a distinct trend from around 642 tonnes in 1992 to 698 tonnes in 2015 (DFO, 2018).

There is concern that European green crab, since initially detected in 2007, may have negatively impacted the lobster resource through predation, competition and habitat modification (DFO, 2016a); and that their continued spread could be detrimental to other areas, particularly the high lobster producing south coast region of Newfoundland (corresponding to LFA 11).

Lobster trap catch rates can be heavily dependent on the behavioural interactions occurring in and around the fishing gear (Jury et al., 2001; Karnofsky and Price, 1989). Importantly, studies have shown that different populations of green crab from distinct source populations can have different ecological impacts on lobster (Haarr and Rochette, 2012). Given that the agonistic interactions between green crab and lobster are complex and context dependent, it is important to study the interactions within the invaded system itself and address mitigation strategies on a site-specific basis.

For the lobster fishery, we have not yet identified a clear causal pathway that links green crab invasions to reduced catches. One hypothesis is that green crab directly interfere with the lobster capture process, either by depleting the bait, by occupying the trap and impeding lobster entry, or by actively defending the trap against lobster entry.

The main objectives of this research are two-fold. First, the project will determine whether green crabs co-occur with lobsters in traps based on underwater trap video data and concurrent green crab/lobster catch data. The second objective is to assess the nature of the behavioural interactions that occur within traps between green crabs and lobsters. Specifically, we will examine three hypotheses. First, that green crabs are accessing the trap earlier in the soak period than lobsters. Second, that green crabs rapidly deplete the bait, thereby removing the incentive for lobsters to enter the trap. Third, that green crabs impede lobster entry by actively defending the trap opening. We also aimed to examine whether these interactions differ between wooden and wire lobster traps. Both wooden and wire traps have escape slats from which crabs and undersized lobster can enter/exit, however wooden traps have wider, elongated slats, compared to the smaller, square cells of the wire traps which could enhance trap accessibility for green crab bycatch.

We sampled in five distinct invaded regions across Newfoundland. This allowed us to assess the prevalence of green crab and lobster co-occurrence in nearshore lobster fishing areas. At each site we used underwater video cameras attached to both wooden and wire lobster traps, observing the traps in situ over continuous 12 hour soak periods to collect quantitative data to test our hypotheses.

In this chapter we describe the process we underwent in designing and constructing the custom-built camera system that enabled us to record underwater videos.

We then outline our field methods, and describe how we used the videos recorded during the field season to answer the questions posed above.

1.3 Materials and Methods

1.3.1 Camera Apparatus

We used an underwater video system consisting of a low cost, custom made underwater housing which held a Sony Actioncam HDR- AS20 and an Anker 2nd Gen Astro E4 13000 mAh external battery mounted on a removable plate (Bergshoeff et al., 2017). Each camera and external battery was contained within a custom-built camera housing constructed from PVC (schedule 40 thickness) and other readily available parts from McMaster Carr. Each case had a ½” thick acrylic window on the front, and a domed, removable cap on the back. A waterproof face-seal was formed between the main camera housing body and the end-cap using an O-ring which was compressed and held in place by three quick-release latches, which allowed easy access to the camera equipment. These camera housings were pressure tested in a hydrostatic test chamber to 100 m depth to ensure structural and functional integrity. Finally, the camera and battery setup was mounted on a removable PVC plate, which was secured within the camera housing using industrial-strength Velcro. This allowed for easy removal and stable placement of the camera equipment within the housing.

We selected the Sony ActionCam HDR- AS20 for their ability to record high quality videos, (including excellent low-light performance and a wide 170° field of view), compatibility with high-capacity memory cards and their inexpensive cost. Using a SanDisk Ultra 128 GB Micro SDXC memory card, the camera was capable of recording for 13 hours continuously in high definition (1080p). The camera would automatically stop recording at 13 hours due to internal firmware restrictions. On the internal battery alone, the camera would only be able to record for two hours, therefore we used an Anker Astro E4 13,000 mAh external battery to enable the camera to record for the full 13 hour maximum. Finally, we paired the cameras with a Sony RM-LVR1 Live View Remote, a device which we used to operate the cameras via wifi connectivity once they were sealed inside their respective camera housings. Although not essential for the operation of the unit, this tool allowed for precise alignment of the camera's field of view (FOV) in order to maintain consistency across videos, and a simple way to start recording at the time of trap deployment. We attached each camera system to a wooden frame built around a standard lobster trap, and secured the housing with a 114-165 mm diameter gear-clamp.

Collecting video data during overnight trap deployments required an external lighting system. We used two Light and Motion GoBe+ flashlights with red LED focus heads with battery life sufficient to provide lighting for the entire night cycle. We used red lights in order to minimize the behavioural impact of full-spectrum light on crustaceans, as many are insensitive to wavelengths greater than 620nm (Nguyen et al., 2017); however, image quality was affected with the red light due to high absorption of this frequency in water (Williams et al., 2014). We used SanDisk Ultra 128 GB Micro SDXC Class 10 cards for storage. Using this setup we were able to switch out the battery and storage cards without having to go back to shore enabling an efficient turnover between day and nighttime deployments.

The camera housing was mounted on a wooden frame constructed around standard wood and wire lobster traps. The camera housing system was secured to the frame with a 114-165 mm diameter gear clamp. The camera was oriented facing downward above the trap, allowing for a top-down view. The camera was positioned at a height of 58 cm above the top of the trap, and 100 cm above the ocean floor, creating a field-of-view (FOV) of approximately 105 cm by 170 cm when underwater. This setup allowed us to view both the area surrounding, and inside of the trap. We attached scuba compasses to each camera-rigged trap to determine the trap orientation from the videos.

Overall, the system was capable of recording continuous 1080p high definition video for 13 hours, capturing lobster and green crab approaches within the field of view as well as entries, exits, feeding and intra/interspecific behavioural interactions.

The design of our trap camera system allowed us to deploy three camera traps and two standard traps using a 3.5 m zodiac.

1.3.2 Trap deployments

All sites were located in green crab invaded, nearshore lobster fishing areas around Newfoundland. We deployed lobster traps in five distinct green crab-invaded areas between June and July 2015. Sites sampled in 2015 include: Fair Haven, Placentia Bay (June 9-11), Little Harbour East, Fortune Bay (June 22-26), St. George’s, St. George’s Bay (July 7-10), Deer Arm, Bonne Bay (July 11-14) and Penguin Arm, Bay of Islands (July 14-15) (Figure 1.1). All traps were deployed in 1-10m of depth.

Each set of deployments consisted of three camera-rigged traps (two wire traps and one wooden trap) as well as two standard traps (one wire trap and one wooden trap).

This allowed us to examine whether the camera apparatus and trap type (wooden/wire) affected catch rates.

In order to ensure that the camera field of view was centered correctly, we used a wireless Sony RM-LVR1 Live View Remote to make fine adjustments to the orientation of the housing. Traps were baited with approximately half a frozen herring in mesh bait bags attached within the parlour end of the trap and fished for approximately12-hour soaks to obtain both day and nighttime trap catch and video data. In some cases logistical factors including weather and travel affected trap deployment or retrieval times, contributing to variations in soak time. Upon trap retrieval, lobsters captured were measured and sexed before being released at the same site from which they were caught. Green crabs were measured and sexed before being euthanized by freezing and all other bycatch was recorded prior to release.

After the standard traps were hauled they were re-baited and immediately re-deployed. For the camera-rigged traps, the battery and memory cards were removed and replaced on the boat before being re-deployed.

The Institutional Animal Care Committee at Memorial University approved this project as a ‘Category A’ as only invertebrates were involved. Field research was conducted under experimental licenses NL-3133-15. Issued by DFO.

1.3.3 Video analysis

Trap videos were scored manually using a standardized procedure to evaluate the video footage obtained during the 2015 field season. Video files were viewed using VLC

Media Player 2.2.1 on a 27-inch 16:9 (widescreen) flat screen monitor. We began analyzing the video as soon as the trap landed on the seafloor.

We recorded lobster and crab behaviours using a procedure similar to Favaro et al. (2014) and Jury et al. (2001). Specifically, we recorded the following behavioural categories for lobster, green crab, and rock crab:

1) Approach – any individual entering the FOV of the camera. Direction of approach was also recorded. Given that most organisms were not individually identifiable the same individual may have been counted multiple times as they exit and re-enter the field of view.

2) Entry Attempt – success/failure as well as time for each success/failure.

3) Exit – any individual leaving the trap, location of exit was also noted (entrance or escape vent).

We watched especially for behaviours that could indicate an interaction between green crab and lobster. These included green crab emptying the bait can, and green crab engaging in agonistic behaviours targeted at lobster in or around the traps.

1.3.4 Statistical analysis

Determining the effect of camera presence on catch:

We deployed traps with cameras along with traps without cameras to act as controls. For both wooden and wire styles of lobster traps, the traps with and without cameras were deployed in the same general area, but were not directly paired.

Camera, trap type, and soak duration effects for lobster catch:

To determine if there was a difference in catch between both the type of lobster trap and the presence of the camera apparatus we performed Welch's two sample t-tests. This type of test is an adaptation of the Student's t-test and is more reliable when the two samples have unequal variances and sample sizes (Ruxton, 2006). To assess whether there was a relationship between lobster catch and the amount of soak time we performed a bivariate linear regression of the number of lobster captured in traps against the duration of time traps were soaking in the water [Equation (1)]. We verified model assumptions by plotting residuals versus fitted values.

$$\text{Lobster catch}_i \sim N(\mu_i, \sigma^2)$$

$$E(\text{Lobster catch}_i) = \mu_i$$

$$\text{Var}(\text{Lobster catch}_i) = \sigma^2$$

$$\text{Lobster catch}_i = \beta_o + \beta_1 \text{Soaktime}_i$$

(eqn 1)

1.4 Results

1.4.1 Field Deployments

During the 2015 field season, a total of 54 camera traps (19 wooden and 35 wire type traps) and 40 traps without cameras (20 wooden and 20 wire type traps) were deployed (total n=94) across the five field sites. Trap deployment times ranged from 4.1 to 25h (mean ± 1 S.E. = 12.9± 0.52).

The number of lobster caught per trap as well as the fishing effort varied across the five study sites visited in 2015 (Table 1.1). Of all five sites that we sampled, only deployments in Little Harbour East (Fortune Bay) and Penguin Arm (Bay of Islands) had mean lobster catches greater than one (Table 1.1; Figure 1.2). Bycatch at each location was generally low (Table 1.2). The most common occurrence of bycatch was rock crab in St. George's Bay (Table 1.2). Due to the fact that our sample size is limited for the Penguin Arm site (n=3), we only refer to data collected from the Fortune Bay Site for the analysis below.

We found no significant impact of either the presence of the camera apparatus ($t= 0.1595$, $df= 23.439$, $p= 0.8746$), or the lobster trap type (wooden/wire) ($t= 0.4923$, $df= 30.752$, $p= 0.626$) on lobster catch in Little Harbour East (Fortune Bay) (Figure 1.3 and 1.4). Additionally, we did not detect a relationship between the amount of time a trap was soaking in the water and the number of lobster caught (adjusted $R^2= -0.0291$, $F_{1,31}= 0.09284$ $p= 0.763$) (Figure 1.5).

Camera traps fished in Little Harbour East, Fortune Bay (n=17) caught between 0 and 7 lobsters (mean= 1.47 lobsters; SD= 2.12), and non-camera traps fished in Little Harbour East (n= 16) caught between 0 and 4 lobsters (mean= 1.56 lobsters; SD= 1.03). Wire traps fished in Little Harbour East, Fortune Bay (n= 19) caught between 0 and 7 lobsters (mean= 1.63 lobsters; SD= 1.92), and wooden traps fished in Little Harbour East (n=14) caught between 0 and 4 lobsters (mean=1.36 lobsters; SD= 1.28).

Only two green crab were caught across all deployments, one in Little Harbour East and one in Fair Haven. These individuals fell out of the traps as they were pulled aboard as they were small enough to fit between the gaps in the trap slats/escape vents. There was no observed co-occurrence between green crab and lobster in either the underwater videos (with the exception of one video) or the catch data.

1.4.2 Video analysis

We observed a total of 792 lobster approaches over the course of 18 camera deployments (approximately 150 hours of video analyzed) (Table 1.3). From the underwater video we observed considerable variability between the number of lobster that approached the trap and those that entered (Table 1.3). Across videos in Little Harbour East (Fortune Bay) we observed a total of 112 entry attempts. Of those attempts, 37.5% (N = 42) were successful (Table 1.3). Of those lobster to successfully enter, 66.6% (N = 28) were able to exit the traps prior to retrieving the gear (Figure 1.6; Table 1.3). Large lobster (those that could not escape through the trap cells/wooden slats) once inside the trap, seem to be retained for the duration of the trap soak. No exits have been observed through the trap entrance. Some individuals were able to access the trap through the wooden slats or escape panels (for the wire traps), exiting the same way through which they entered. Notably, some individuals entered far enough to feed but never fully enter the trap; a behaviour that has been previously described by Karnofsky and Price, (1989).

Rock crabs were observed in many of the videos entering the traps and accessing the bait. For the most part these individuals could readily enter and exit the traps given their smaller size and ability to fit through the gaps in the trap. In a couple of instances, lobster already within the trap seem to impede the entry of other lobster through their aggressive behaviour. In some cases individuals seem to defend the bait from other individuals both within and outside of the trap.

In videos from Little Harbour East (Fortune Bay) we observed a total of 4 green crab approaches, 6 entry attempts/successful entries, and 5 exits. No green crab were observed in trap videos at any other site. Similarly to rock crab, green crab could readily enter and exit the traps through the wire cells/wooden slats.

Generally, lobster seem to be slow to find the trap entrance and many individuals have been observed circling the trap and attempting entry through the rear side, inserting their claws through the gaps. In some cases smaller lobster have been seen to enter the trap through these gaps.

Bycatch was generally low in our underwater videos, however in one deployment a sculpin entered the trap and in subsequent hours was eaten by two large lobster inside the trap.

1.5 Discussion

Overall, the findings of this analysis suggest that lobster catch varies according to site but is not significantly influenced by either the underwater camera rig or the trap type. Lobster catch was highest in Fortune Bay (Little Harbour East) and Penguin Arm (Bay of Islands) and lowest in Fair Haven and Bonne Bay. Each site we sampled had a different green crab invasion history, Fair Haven being the earliest (2007) and Fortune Bay being the most recent (2014). No lobster were caught in Fair Haven over the duration of our field study. Given that lobster landings in this area (Placentia Bay) have declined by around 80% since the early 1990's it is perhaps unsurprising that lobster catch was low in this area.

In our study lobster catch was not found to be influenced by the underwater camera rig. This eliminated the apparatus itself as a factor influencing lobster catch. In addition, lobster catch did not vary according to wooden and wire trap types.

Interestingly, catch data showed no overlap between green crabs and lobsters. In total we caught two green crab across all sites and deployments and observed two green crabs across all the videos analyzed. In general, the co-occurrence between lobster and green crab in the videos was extremely low (1 instance). This prevented us from assessing the behavioural interactions between green crab and lobster at the level of the gear.

The quality of the videos that we recorded was extremely high, and our pressure cases were largely reliable when used correctly. This will enable us to effectively conduct future studies using this technique, as we now have a demonstrated capacity to conduct long-duration video-based studies of traps in the subtidal environment. It was more difficult to record high quality video at night, as a result of the dim illumination around the periphery of the field of view. We expect this limitation could be improved through the use of additional red lights.

Our study took a novel approach to understanding the interactions between lobster and green crab inside and around fishing gear, representing one of the first of its kind to study this *in situ* using underwater video. Our results from 2015 showed little co-occurrence between lobster and green crab in both catch and video data. There are at least three possible explanations for these preliminary findings regarding lack of concurrent capture between green crab and lobster. First, annual variation of green crab populations and various environmental factors, including above normal sea ice extent and a late spring warming DFO, (2016b) may have contributed to low population densities of green crab in some areas. Studies have demonstrated that unseasonably low winter temperatures can result in widespread mortality of adult green crabs, and low recruitment (Berrill, 1982; Crisp, 1964), particularly in more shallow coastal areas such as sites on the West Coast of Newfoundland (C.H. McKenzie, Research Scientist, Department of Fisheries and Oceans (DFO), personal communication, May 2018). It is therefore possible that these low temperatures contributed to reduced catches in certain areas compared with previous years (Yamada and Kosro, 2010).Second, we may have deployed lobster traps in unsuitable sites. Each deployment site was informed by local experts, including fishermen, who reported catching both green crab and lobster in these areas. However, Green crab patchiness and population vary greatly by habitat and location and could have influenced the low co-occurrence observed.

A third possible explanation for our results was that, in general, green crab and lobster do not actually co-occur in fishing gear and, as suggested in anecdotal reports, may only interact in areas where green crab population densities are particularly high.

The focus of our next field season was to investigate whether the presence of green crab inside lobster traps would impact the rate at which lobster would enter and be captured by the fishing gear. We directed this research towards repeating 2015 field season methods, and selecting sites that enabled us to further investigate whether green crab commonly co-occur with lobster in lobster traps. We aimed to test the hypothesis that 2015 was an abnormal year. Additionally, we aimed to identify fishing locations with confirmed overlap of green crab and lobster. This was informed by both local knowledge as well as the results from our 2015 study.

Direct impact on lobster catch and trapping may only be one factor. The impact that green crab are having on the lobster fishery within the broader ecosystem, rather than at the level of capture by the gear itself, may be of greater influence. It may be more productive to focus our attention on understanding the broad impacts that green crab can have on marine ecosystems, including habitat degradation (Garbary et al., 2014; Matheson et al., 2016).

Our study highlights how underwater video can serve as a powerful tool to fill the gaps in what we are unable to glean from catch data alone, creating a more complete picture of what is going on when a trap is in the water by maximizing behavioural information. This research provides the information necessary to design future quantitative studies involving the impact of invasive green crabs on the catchability of lobster which we examined during a second field season in 2016.

Tables.

Table 1.1. Summary of lobster caught at each site in 2015

Location	Deployments (n)	Mean catch	Standard deviation	Minimum catch	Maximum catch	Total catch
Fair Haven	8	0	0	0	0	0
Bonne Bay	25	0.08	0.277	0	1	2
Little Harbour East	33	1.515	1.661	0	7	50
Penguin Arm	3	1.667	0.577	1	2	5
St. George's Bay	25	0.32	0.557	0	2	8

Table 1.2 Summary of all bycatch species caught at each site in 2015.

	Fair Haven	Bonne Bay	Little Harbour East	Penguin Arm	St. George's Bay	All Sites
Rock Crab (Cancer irroratus)	1	13	1	0	38	53
Cunner (Tautogolabrus adspersus)	0	3	0	0	0	3
Sculpin sp. (Myoxocephalus sp.)	1	1	0	1	1	4
Green crab (Carcinus maenas)	1	0	1	0	0	2

Table 1.3. Camera trap summary for ~150 hours of analyzed video from sites in Fortune Bay (Little Harbour East) (n=12), Bonne Bay (n=2) and Fair Haven (n=4). All counts are from Fortune Bay (Little Harbour East) except for two approaches in Bonne Bay.

	Total Approaches	Total Entry attempts	Total successful entries	Total exits	Total catch
Lobster	**792**	**112**	**42**	**28**	**9**
Green crab	**4**	**6**	**6**	**5**	**1**

Figures.

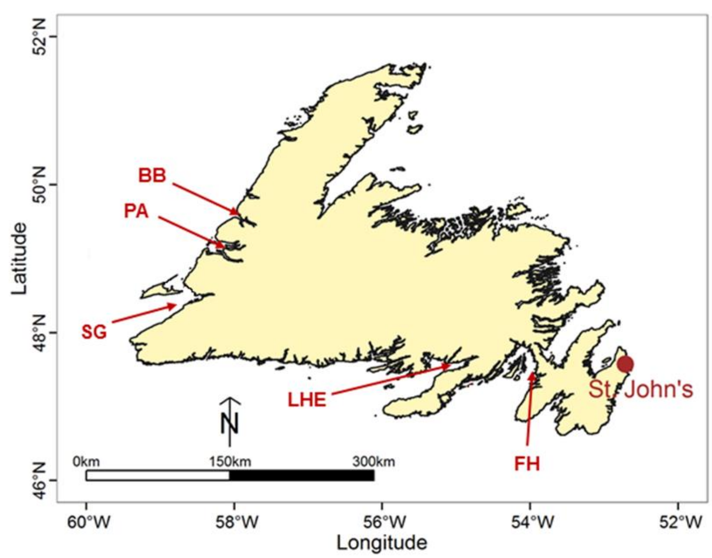

Figure 1.1. Map of 2015 study sites across Newfoundland. Sites included Bonne Bay (BB), Fair Haven (FH), Little Harbour East (LHE), Penguin Arm (PA), and St. George's Bay (SG).

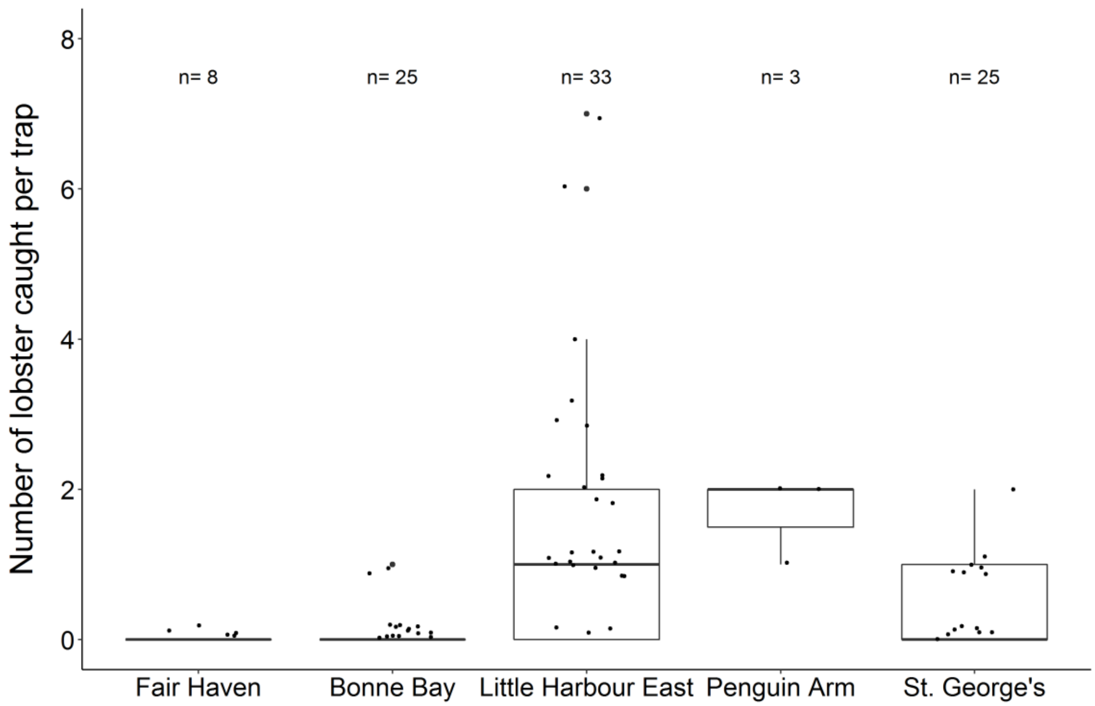

Figure 1.2. Comparison of lobster catch across five different sites (Bonne Bay, Fortune Bay, Fair Haven, Penguin Arm, and St. George's bay). The number of trap deployments is shown in the numbers above each boxplot.

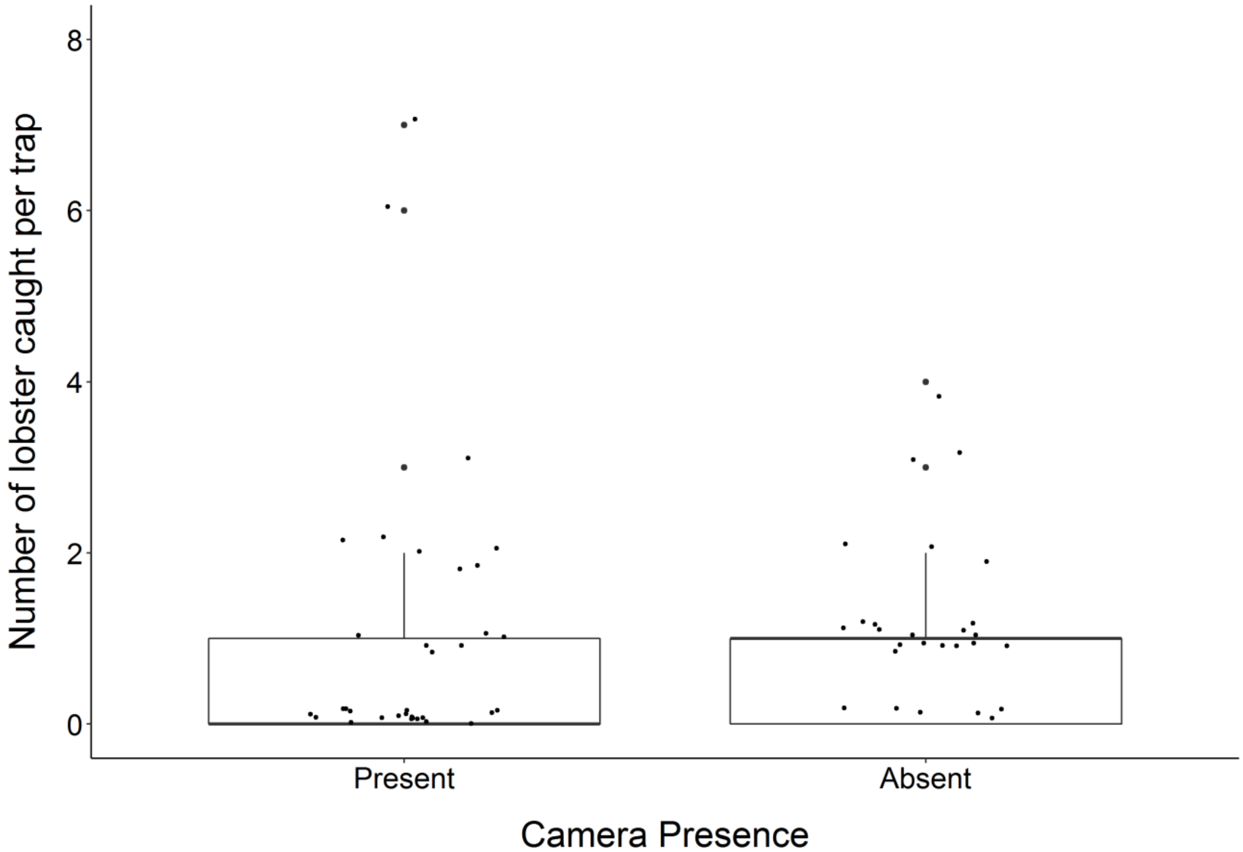

Figure 1.3. Comparison of lobster catch according to camera presence on the trap in Little Harbour East, Fortune Bay.

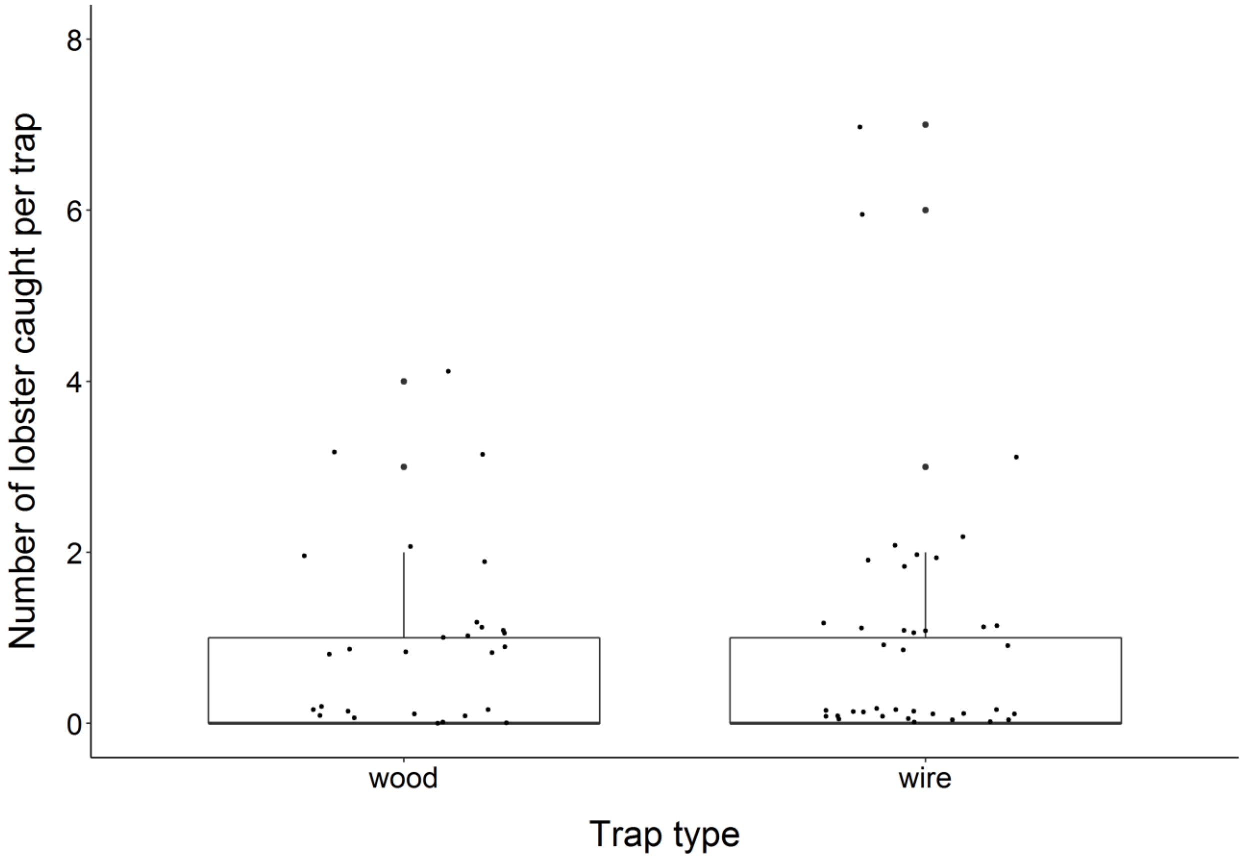

Figure 1.4. Comparison of lobster catch for wooden and wire trap types in Fortune Bay.

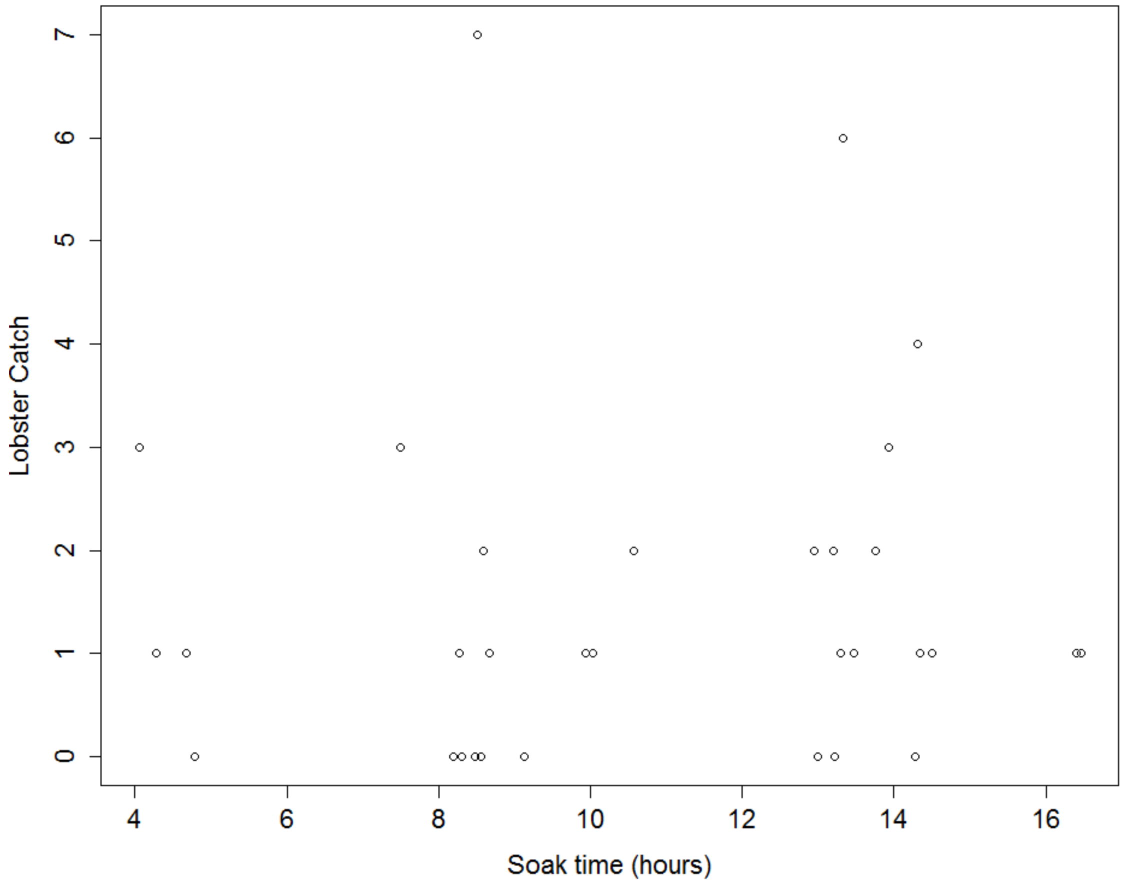

Figure 1.5. Lobster catch according to the trap soak period for deployments in Fortune Bay.

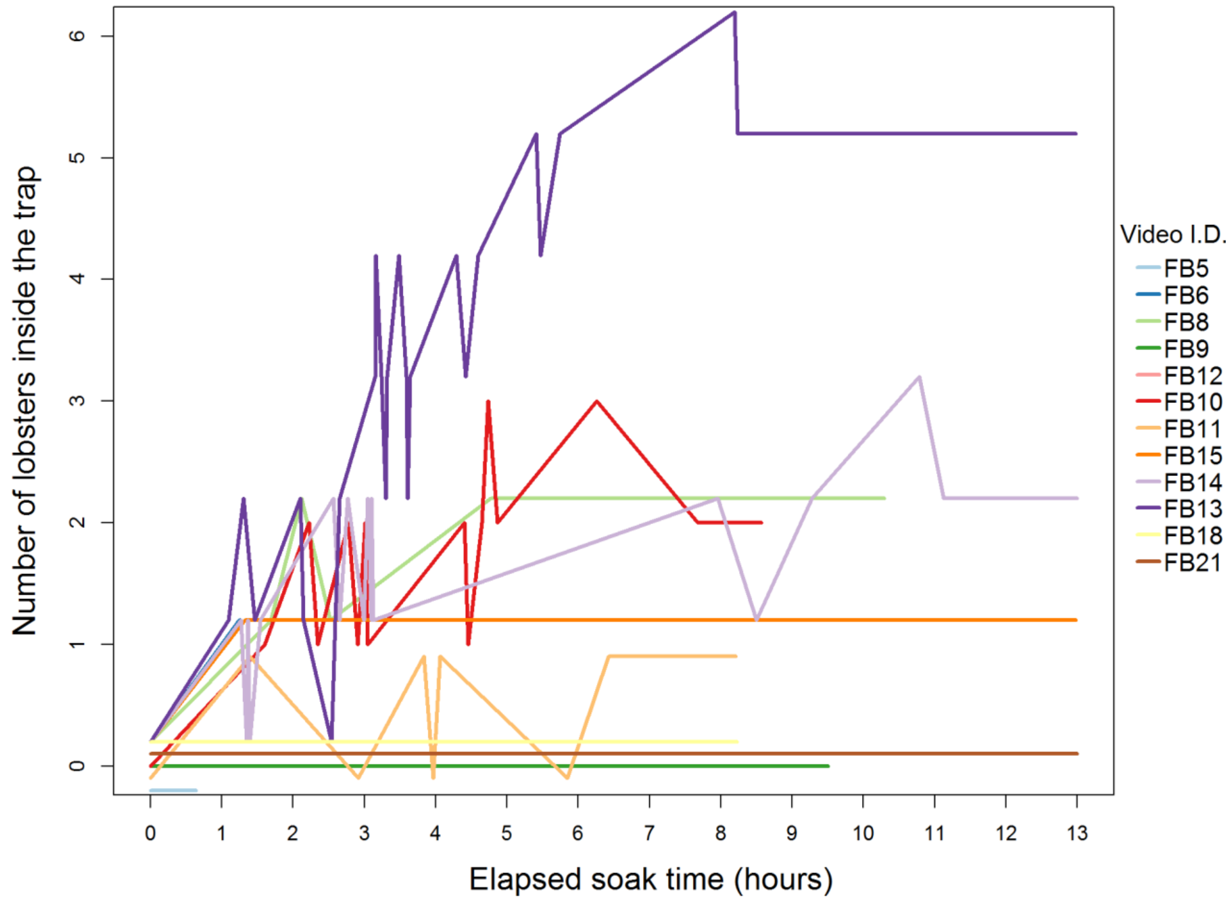

Figure 1.6. Lobster accumulation over the course of each trap deployment (n= 12) for all successful entries and exits. Each coloured line represents an individual trap deployment in Little Harbour East, Fortune Bay (FB). Lines are jittered so as not to overlap.

Chapter 2.

Investigating the impact of invasive green crab (*Carcinus maenas*) on American lobster (*Homarus americanus*) catch efficiency using underwater video, SCUBA and tethering techniques.

2.1 Abstract

Species invasions pose a global threat to marine biodiversity. European green crab (*Carcinus maenas*) are one of the most successful marine invaders worldwide and have been discovered in the coastal waters of southern and western Newfoundland and Labrador. Impacts of green crab on the American lobster (*Homarus americanus*) are not well understood, particularly for interactions around deployed fishing gear. Declines in lobster catch rates in invaded systems have prompted concerns among lobster fishers that green crab are interfering with lobster catch. Here, we examined the impact that invasive green crab have on the lobster trapping process, focusing on whether they influence entries into traps, deplete bait, or promote exit of lobsters from traps prior to capture. We conducted a field experiment in Fortune Bay, NL, in which we deployed lobster traps pre-stocked with either green crabs, native rock crabs (*Cancer irroratus*), a procedural control), or nothing (control). From these traps, we compared lobster catch rates and factors associated with entry and exit from traps (as determined by the use of underwater cameras). In addition, we used SCUBA surveys to determine whether the ambient density of lobster and green crab in the ecosystem affected catch processes. We found: 1) the presence of crabs can impact the total number of lobster that will attempt to enter the trap as well as the number that do so successfully, 2) this effect is not species specific and applies to both native rock crab and invasive green crab, 3) lobster will predate on green crab, rock crab and other lobster inside traps and 4) there is a positive association between lobster catch and ambient lobster density. Our data suggest that the relationship between in-trap green crab density and trap effectiveness is linked though not specific to non-native versus native crab species.

2.2 Introduction

Species invasions pose a global threat to marine biodiversity (Carlton, 2000), and present substantial ecological and economic challenges (Sala et al., 2000). The European green crab (*Carcinus maenas*) has invaded intertidal and subtidal habitats across the world (Klassen and Locke, 2007), and occupies a wide range of habitats within sheltered areas of intertidal and estuarine zones (Ray, 2005). Its tolerance for wide ranges of salinity, oxygen, temperature, and habitat type along with its high fecundity and propensity for omnivory make it an excellent invader (Klassen and Locke, 2007). Green crab are able to tolerate temperatures between 0 and 35 degrees Celsius and salinities ranging from 4 to 52‰ (Cohen et al. 1995). As generalist predators they consume a diverse diet of marine macrofauna including juvenile fishes, crustaceans, bivalves, gastropods, nematodes, and polychaetes (Cohen et al., 1995).

Invasive species such as green crab exhibit high phenotypic plasticity allowing them to alter their morphology, physiology and behaviour to adjust to different environments (Henry et al. 1999). This is in contrast to native species, such as the American lobster (*Homarus americanus*), which is constrained by salinity and temperature (Jury et al. 1994; Crossin et al. 1998). In light of human-mediated climate change, populations of green crab are likely to further expand as a result of increasing sea temperatures, which can enhance their growth and reproduction (Smith et al. 1955; Brown et al. 2004), as well as open up previously unavailable habitat (specifically those with cold water temperatures) to invasion (U.S. Environmental Protection Agency (EPA), 2008).

Owing to their propensity to invade new ecosystems and the severity of their impacts once invasion occurs, the European green crab is ranked among the 100 ‘worst alien invasive species’ in the world (Lowe et al.2000). Green crab first invaded Atlantic Canada in 1951 but their establishment in the nearshore waters of Newfoundland has been comparatively recent (Klassen and Locke, 2007). They were first detected in North Harbour, located in Placentia Bay, Newfoundland in 2007. Invasive green crab have been implicated in the degradation of eelgrass beds (Garbary et al. 2014; Matheson et al. 2016), declines of soft-shelled clam (*Mya arenaria*) populations (Bryan et al. 2015), as well as having negative impacts on oyster (*Crassostrea virginica*) and mussel (*Mytilus edulis*) beds (Curtis et al., 2012; DeGraaf and Tyrrell, 2004; Miron et al., 2005).

Since 1992, lobster landings in Placentia Bay have severely declined from 427 t to 20 t in 2017, representing an 80% decline in an area that was once the most productive lobster fishing area in the region (DFO, 2018). While the decline clearly began before the onset of a green crab invasion, the presence of the invasion may complicate lobster recovery in Placentia Bay. Further, the expansion of green crab into other bays has raised concern that additional damage to the lobster stock may occur (DFO, 2016a).

Fortune Bay, located adjacent to Placentia Bay along the south coast of Newfoundland currently accounts for 40% of lobster landings across all nine active lobster fishing areas in the province (DFO, 2016a), and contains many eelgrass (*Zostera marina*) meadows along its shores. Invasive green crab were first detected in Fortune Bay in 2014. Their presence in near-shore coastal estuarine environments has been associated with the damage and destruction of eelgrass beds as a result of their tendency to dig and burrow within the sediment while foraging, causing damage to eelgrass roots and rhizomes (Garbary et al., 2014; Neckles, 2015). Eelgrass meadows create structurally complex habitats which support diverse biotic communities and provide important ecological services including nutrient cycling, shoreline stabilization, and carbon sequestration (Kenworthy et al., 2006; Orth et al., 2006). As a result, eelgrass has been deemed an ‘ecologically significant species’ in Canada (DFO, 2009).

Fisheries and Oceans Canada Science has conducted research trials in partnership with the fish harvesters union (FFAW) to determine the impacts of the green crab invasion through active trapping and removal (DFO, 2011). These trials in Fortune Bay have been based on removals using Fukui traps (described in Methods). DFO has used this technique on both the Pacific and Atlantic coasts of Canada to supress green crab populations (Duncombe and Therriault, 2017). However, as with all marine invasions, complete eradication is likely impossible (Bax et al., 2003; Thresher and Kuris, 2004).

Green crab can impact lobster populations through a variety of mechanisms. For example, Rossong et al. 2011, found that juvenile lobster in aquariums that contained green crab favoured shelter use over feeding. This behavioural impact, which was absent in aquariums without green crab, resulted in reduced energy intake. Other laboratory studies have indicated that green crab predate on juvenile lobster (Rossong et al. 2006), and outcompete sub-adult lobster for a limited food source (Williams et al. 2006).

It is not clear whether observed declines in lobster catch rates in invaded ecosystems are due to a reduction in lobster abundance, or because green crab are interfering with the capture process itself (or a combination of both are factors).

Interactions between green crab and lobster are not well understood, particularly for interactions that occur in the vicinity of deployed fishing gear (Goldstein et al. 2017). Research in the field has shown that not only do green crab and lobster overlap in some lobster fishing areas, but a considerable number of green crab will enter and be captured by lobster traps. Over a two year study with 248 individual trap deployments, Goldstein et al. 2017 caught approximately 8.5 times more green crab than lobster. Though it is unlikely that larger lobster are vulnerable to green crab predation (Goldstein et al. 2017), trapping inefficiencies , have been associated with dominance relationships and territorial behaviour between individuals within a target species (Jury et al. 2001). It is therefore possible that the presence of green crab inside lobster traps could influence the number of lobster that subsequently enter the trap as a result of interspecific interactions inside and around the gear.

In this study, we conducted a series of field experiments to determine whether green crab had a direct impact on the ability of commercial lobster traps to catch lobsters, and to identify the mechanism by which this impact may be occurring. We employed three pre-stocking conditions (traps with green crab, traps with native crab, and traps with no pre-stocked crabs) to assess the impact that green crab had on lobster catch rates, and if such an impact was present, to determine whether it was unique to the invasive species or whether it occurred with native crabs as well. In addition, we used a custom-built underwater video camera (Bergshoeff et al. 2017) to observe the stocked and unstocked traps for 12 hours during deployments to determine the mechanism(s) by which green crab could influence lobster catch. Finally, we conducted SCUBA surveys around the deployed camera traps to assess the extent to which our observations were mediated by the densities of lobster, green crab, and native crab in the vicinity of deployed gear.

We tested three non-exclusive hypotheses: First, that traps pre-stocked with green crab would catch fewer lobsters per deployment than unstocked traps, and that the camera would have no detectable impact on catch rates. Second, as determined by results from our video-based data, that one (or more) of the following mechanisms were present in deployed traps: a) green crab invade the trap early in a deployment, deplete the bait, and thereby reduce the numbers of lobster that approach the trap. b) green crab invade the trap early in a deployment and subsequently block the trap entrances to future lobster entry (i.e. lobster approach, but do not enter). c) green crab enter traps after lobsters, thus forcing trapped lobsters out of the gear (i.e. green crabs are associated with an increase in exit rates from the trap). Third, that green crab induced reductions of lobster catch would be stronger for gear deployments where the ambient green crab density was higher.

2.3 Materials & Methods

2.3.1 Specifications of camera apparatus

To record underwater video of lobster traps fishing *in situ* we designed and constructed a low-cost camera system capable of recording full high-definition videos for 13 continuous hours at 1080p resolution. This system is detailed in Bergshoeff et al., (2017). We mounted the camera housing to a wooden frame constructed around standard commercial single-parlour wire-mesh (3.8cm mesh size) lobster traps. We secured the housing to the frame with a 114-165 mm diameter gear clamp and oriented the camera to face downwards above the trap. We positioned the camera at a height of 58 cm above the top of the trap, and 100 cm above the ocean floor, creating a field-of-view (FOV) of approximately 105 cm by 170 cm when underwater. This allowed for the top-down viewing angle necessary to quantitatively study lobster behaviour inside and around the trap. Using this setup we were able to observe lobster entering, exiting, inside the trap, as well as those around the trap for 13 continuous hours. We deployed the traps at depths shallow enough for ambient light to illuminate the pot during the day, therefore we did not use external lights.

2.3.2 Study site and fieldwork

We conducted our field work in nearshore lobster fishing areas around Little Harbour East and Little Bay East, Fortune Bay on the southern coast of Newfoundland (Figure 2.1) for five weeks between July-September 2016, directly following the closure of the two month lobster fishery in LFA 11 (DFO, 2016a). This allowed us to carry out our field experiments and SCUBA surveys without interfering with local fishing operations or having to work around other fishing gears and vessels. We selected sites based on advice from fishers, scientists (K. Matheson, Aquatic Science Biologist, Department of Fisheries and Oceans (DFO), personal communication, June 2016), and local members of the community.

We deployed all traps at depths ranging from 3 to 15 m. All traps were deployed from a 4.2 m zodiac. Each set of deployments consisted of three camera-equipped traps (each of which were assigned one of three pre-stocking conditions, described below) as well as two lobster traps without attached cameras. Prior to each deployment we baited the traps with equal amounts of frozen herring (about one half of a large fish), in mesh bait bags tied inside the kitchen (entrance compartment) of each trap (Figure 2.2). Once the traps were baited, we mounted the camera components inside the housings. We oriented the field of view for each camera and initiated video recording using a wireless Sony RM-LVR1 Live View Remote prior to each deployment. Soak times (i.e. the amount of time between deployment and retrieval) were approximately 24 hours and traps were set ~50 m apart. No other fishing activity was going on in the vicinity of our experiment for the duration of our fieldwork. Upon retrieving the traps, we determined the sizes (carapace length) and sexes of all lobster captured before releasing them at the same site from which they were caught. We counted any green crab captured and placed them into collection bags for disposal on shore. After hauling the standard traps we re-baited them and immediately re-deployed the traps. For the camera-rigged traps, in addition to re-baiting the traps, we also removed and replaced the batteries and memory cards. We recorded GPS coordinates for each trap deployment and downloaded the videos onto portable hard drives once back on shore.

The project was approved as a ‘Category A’ study by the Institutional Animal Care Committee at Memorial University as it only involved invertebrates, and all field research was conducted under experimental license NL-3271-16 issued by Fisheries and Oceans Canada.

2.3.3 Pre-stocking field experiment

To determine the influence of crabs (both native and invasive) inside the trap on subsequent lobster entries, we ‘pre-stocked’ two of the three camera-equipped traps with either seven native rock crab (*Cancer irroratus*) or seven invasive green crab (*Carcinus maenas*) tethered inside the kitchen (entrance compartment). The density of pre-stocked crabs (seven) was selected to maximise crab presence in the kitchen whilst not over-crowding the tethered individuals leading to the fishing line (tethers) becoming tangled. The technique of tethering has been described in previous studies to evaluate behavioural interactions among species (Wahle and Steneck, 1992; Watson and Jury, 2013). We tethered the crabs using fine fishing line looped around the rear legs of the crab and tied (leash-like) to split metal rings attached to the wire cells on the top of the kitchen (Figure 2.2). This allowed the crabs to move freely around the kitchen without being able to exit the trap. The third camera trap served as a control and was not pre-stocked with any crabs. We captured the green crab used for pre-stocking with Fukui traps in the intertidal areas bordering the sites where we deployed our lobster traps. We collected rock crab via SCUBA from areas around our deployment sites. All tethered crabs (both green crab and rock crab) had carapace widths > 5 cm. Each crab was used in only a single experimental trial, and was either destroyed (green crab) or returned to the site from which they were collected (rock crab).

2.3.4 SCUBA surveys

We conducted a total of 33 individual dive surveys in July and September 2016 to assess the relative abundances of lobster, green crab and rock crab around deployed camera traps. Due to logistical limitations we were only able conduct dive surveys for 11 of 17 deployments (3 surveys per deployment- one on each camera trap). Divers collected data along four transects oriented North, South, West and East of each trap (Figure 2.3).

For each survey, two SCUBA divers descended on camera traps, one diver clipped a carabiner to the trap and reeled the transect line out, orienting in one of the four cardinal directions. The other diver swam along one side of the transect tape and recorded counts of lobster, green crab and rock crab within two metres of the transect line up to the end of the transect at 25 m. After 25 m the divers swam back to the trap and reeled in the transect tape. This process was repeated, orienting in the remaining three directions. We repeated this for each camera trap. In total 600m^2 were surveyed for each set of trap deployments. We used the data collected from our SCUBA surveys to provide a context for what we observed in our catch and video deployment data when they were matched temporally.

2.3.5 Video analysis:

Following the field study we scored the videos manually, following protocols described in previous literature (Favaro et al. 2012; Jury et al. 2001; Meintzer et al. 2017). Specifically, we recorded the following quantitative parameters for lobster, rock crab and green crab: (1) the number, direction and duration of entry attempts as well as the proportion of those entries that were successful versus failed, (2) the number, direction and duration of exits from the trap, (3) the time spent feeding on the bait, (4) the number and duration of interspecific aggression events, and (5) the number and duration of predation events.

We defined an entry attempt as an instance where more than half the individual's body length crossed inside the trap. The result and duration of each attempt was scored as either failed, where the individual retreated outside the trap, or as a success, where the individual's body crosses entirely into the trap. Individuals could enter/exit the trap through the entrance (E), through the wire cells in the trap kitchen (K) and parlour (P), or through the escape slats in the top (T) and bottom (B) of the trap.

We defined interspecific aggression as agonistic behaviours involving individuals engaging in threat displays including a meral spread (chelae raised and held laterally, outwards from the body), or any physical contact including touching and grasping actions (Haarr and Rochette, 2012; Rossong et al. 2006). We defined predation as behaviours involving one individual being consumed by another. Note, each entry attempt was considered 'new' given that individuals were not individually identifiable, thus we assume that some individuals were counted multiple times.

2.3.6 Statistical Analysis - Catch data

In this paper we use the software package R (R Core team, 2015). We carried out data exploration in accordance with the protocol described in (Zuur et al. 2010).

To model lobster catch as a function of the covariates a Poisson generalized linear mixed-effects model (GLMM) with a log link function was used [Equation (1)]. GLMMs are capable of handling data that would otherwise violate many of the assumptions required for simple linear models and are therefore a powerful technique for the analysis of ecological data (Zuur et al., 2009). The Poisson distribution is typically used for count data and the log link function ensures positive fitted values (Zuur and Ieno, 2016). Fixed covariates in our initial model are trap pre-stocking condition (categorical, four levels: unstocked, green crab pre-stock, rock crab pre-stock, no camera/unstocked) and soak duration (continuous). The interaction terms are trap pre-stocking condition x soak duration.

To incorporate the dependency among observations of the same deployment, we used deployment as random intercept. We then conducted stepwise model simplification, dropping non-significant terms one at a time until all terms in the model were statistically significant (procedure outlined in Crawley, 2012). This procedure was used for all models presented in this paper. The lme4 package (Bates et al., 2017) was used to fit the model. We verified model assumptions by plotting residuals versus fitted values. Residuals met the assumptions for normality, homogeneity and independence, and there was no evidence of overdispersion.

$$
\begin{aligned}
&\mathrm{LobsterCatch}_{ij} \sim \mathrm{Poisson}(\mu_{ij}) \\
&E(\mathrm{LobsterCatch}_{ij}) = \mu_{ij} \\
&\log(\mu_{ij}) = \mathrm{TrapPrestockingCondition}_{ij} + \mathrm{SoakDuration}_{ij} + \\
&\mathrm{TrapPrestockingCondition}_{ij} \times \mathrm{SoakDuration}_{ij} + \mathrm{Deployment}_{i} \\
&\mathrm{Deployment}_{i} \sim N(0,\sigma^2)
\end{aligned}
\tag{eqn 1}
$$

We also examined the size (carapace length) of lobster caught across trap pre-stocking condition (fixed effect, with deployment as a random effect). This was distributed normally, enabling us to construct a simple linear mixed-effects model using the lme4 package (Bates et al., 2017).

2.3.7 Statistical Analysis - Video data

Although catch data can provide us with valuable information about the impact of crab presence inside a trap on lobster catch, they offer no insight into the mechanism by which this impact could occur i.e. why crab pre-stocked traps may affect the amount of lobster captured. To address this, we deployed lobster traps equipped with a custom designed underwater camera apparatus (Bergshoeff et al., 2017). The underwater video component of our study allowed us to evaluate the mechanisms by which green crab could impact lobster catch within the trap. We used a GLMM to test the fixed effect of trap pre-stocking condition on lobster entry time [Equation (2)]. Variability associated with sampling over multiple deployments is incorporated in the model as a random effect. The distribution of our lobster entry time data was best explained by a negative binomial distribution.

$$\text{EntryTime}_{ij} \sim \text{NB}(\text{m}\mu_{ij,}\ \text{theta})$$

$$\text{E}(\text{EntryTime}_{ij}) = \text{m}\mu_{ij}$$

$$\text{Variance}(\text{EntryTime}_{ij}) = \text{m}\mu_{i} + (\text{m}\mu_{i}^{2}/\text{theta})$$

$$\log(\mu_{ij}) = \text{TrapPrestockingCondition}_{ij} + \text{Deployment}_{i}$$

$$\text{Deployment}_{i} \sim N(0,\sigma^{2})$$

(eqn 2)

To examine whether there was an association between trap pre-stocking condition and the proportion of successful versus failed entry attempts by lobster we used the prop.test function in R which uses Pearson's chi-squared test statistic to test the null that the proportions (probabilities of success) in several groups are the same (R Core Team, 2015).

2.3.8 Statistical Analysis - SCUBA data

The SCUBA-based transect survey component of our study provided a context for what we observed in our catch and video data and allowed us to obtain trap-independent estimates of lobster density that were temporally matched to the video and trap catch data. We used a GLMM to measure the impact of the fixed covariates ambient lobster (continuous) and trap pre-stocking condition (categorical, four levels) on lobster catch [Equation (3)]. The interaction terms are trap pre-stocking condition x ambient density. We applied deployment as a random intercept as this models a dependency structure among observations during the same deployment.

The distribution of our catch data was best explained by a Poisson distribution. We simplified the model using stepwise removal of non-significant terms (Crawley, 2012) and fit the model using the lme4 package (Bates et al., 2017). We plotted residuals versus fitted values to verify the model assumptions. Residuals met the assumptions for normality, homogeneity and independence, and there was no evidence of overdispersion.

$$LobsterCatch_{ij} \sim Poisson(\mu_{ij})$$

$$E(LobsterCatch_{ij}) = \mu_{ij}$$

$$\log(\mu_{ij}) = TrapPrestockingCondition_{ij} + AmbientLobster_{ij} + TrapPrestockingCondition_{ij} \times AmbientLobster_{ij} + Deployment_i$$

$$Deployment_i \sim N(0,\sigma^2)$$

(eqn 3)

To examine whether there was an association between trap pre-stocking condition and the proportion of successful versus failed entry attempts by lobster for deployments where video data and SCUBA data were temporally matched, we used the prop.test function in R which uses Pearson's chi-squared test statistic to test the null that the proportions (probabilities of success) in several groups are the same (R Core Team, 2015).

2.4 Results

2.4.1 Catch data

We deployed each of the five traps seventeen times over the duration of our fieldwork for a total of 85 individual trap deployments. Soak times ranged between 15.16 and 26.58 h (mean ± 1 SD = 21.89 ± 3.05). We caught a total of 326 lobster and 6 green crab and 3 rock crab in lobster traps across the entire study.

Trap pre-stocking condition had significant influence on lobster catch for rock crab pre-stocked traps (GLMM: rock crab pre-stock, $\beta = -0.436$, S.E. = 0.175, $z = -2.499$, $p = 0.013$; Figure 2.4A; Table 2.1). We found no significant impact of either the presence of the camera apparatus (GLMM: No camera, $\beta = -0.225$, S.E. = 0.140, $z = -1.610$, p =

0.107; Figure 2.4A; Table 2.1), or the green crab pre-stock treatment (GLMM: green crab pre-stock, $\beta = -0.312$, S.E. = 0.168, $z = -1.855$, $p = 0.064$; Figure 2.4A; Table 2.1) on lobster catch. Model validation indicated our choice of model was appropriate through graphical residual analysis. The model had a dispersion parameter of 1.1, indicating it was not overdispersed. Model output is provided in Table 2.1. Lobster size (carapace length) ranged from 48 to 98 mm (mean ± 1 SD = 80.44 ± 6.08 mm). The average size of lobster caught did not vary significantly across trap pre-stocking condition and 70.9% of the lobster captured were of sub-legal size (< 82.5 mm) (Figure 2.4B).

We did not detect a relationship between the amount of time a trap was soaking in the water and the number of lobster caught across trap pre-stocking condition (Figure 2.5).

2.4.2 Video data

We collected approximately 663 h of underwater video footage across 17 deployments. Of the 663 h of video collected, 452 h had adequate ambient lighting for analysis.

Across all videos we observed a total of 3,801 entry attempts in unstocked, green crab pre-stocked, and rock crab pre-stocked trap pre-stocking conditions. The unstocked trap accounted for 42.8% (N = 1,625) of all lobster entry attempts, whereas green crab and rock crab pre-stocked traps accounted for 27.8% (N = 1,057) and 29% (N = 1,119) of all entry attempts respectively. Of those attempts, 69.7% (N = 1,133) were successful for the unstocked trap, while 45.3% (N = 479) and 49.8% (N = 557) were successful for green crab pre-stocked traps and rock crab pre-stocked traps (Figure 2.6). Of those lobster to successfully enter 94.4% (N = 1,070) were able to exit the unstocked trap, 85.4% (N = 409) exited the green crab pre-stocked traps, and 88.7% (N = 494) exited the rock crab pre-stocked traps prior to retrieving the gear (Figure 2.6).

We did not individually identify lobster as they attempted an entry, subsequently failed, and then re-attempted entry. Therefore, the number of entry attempts recorded does not represent the absolute number of individual lobster that attempted trap entry, as the same lobster may have attempted multiple times.

When we accounted for lobster entry attempts through the entrance only (excluding the small individuals that attempted entries through the wire cells and escape slats) we found 30.1% (N = 139) were successful in the unstocked trap, while 17.1% (N= 106) and 17.7% (N= 105) of entry attempts were successful for green crab and rock crab pre-stocked traps respectively (Figure 2.7).

The proportion of successful entries was higher in the unstocked trap than in either the rock crab or green crab pre-stocked traps for all lobster attempts (x^2 = 190.072, df= 2, $p < 0.001$; Figure 2.8A) as well as for those only through the trap entrance (x^2 = 36.049, df= 2, $p < 0.001$; Figure 2.8B). Smaller lobster were able to easily crawl through the wire cells on the kitchen and parlour sides of the trap, as well as through the escape slats on the top and bottom of the trap. We did not observe any difference in the proportion of successful entries across trap pre-stocking condition for attempts made by small lobster through the wire cells or escape slats (Figure 2.8C). We did not detect any difference in the duration of successful lobster entry attempts through the trap entrances according to trap pre-stocking condition (Figure 2.9; Table 2.2).

There was little difference between the number of lobster inside traps after a full deployment versus at the end of the video analysis period for each trap pre-stocking condition (mean ± 1 SD = unstocked, 1.18 ± 2.46; green crab pre-stock, -0.25 ± 2.86; rock crab pre-stock, -0.47 ± 2.45; Figure 2.10).

Few green crab and rock crab were observed in the trap videos (untethered individuals). Across all 452 hours of video analyzed we observed 45 entry attempts made by green crab, of which 27 were successful. Rock crab made 18 entry attempts, of which 17 were successful. Green crab and rock crab were observed exiting the camera traps 19 and 13 times respectively. The majority of untethered green crab and rock crab were observed in trap videos corresponding to deployments 5 and 6 (Supplementary Table 2.2).

We observed both interspecific and intraspecific predation events across all videos. Lobster were involved as predators in all instances. Of the 60 total events 20 involved tethered adult green crab, 36 involved tethered adult rock crab, and four involved trapped adult lobster). The number refers to predation events (where one individual is being consumed by another) not necessarily the total number of individuals consumed, as many of the preyed upon individuals were consumed by multiple lobsters.

2.4.3 SCUBA Surveys:

Lobster catch was positively associated with changes in the density of lobster on the bottom (GLMM: ambient lobster, $\beta = 0.016$ S.E. = 0.007, $z = 2.258$, $p = 0.024$; Figure 2.11; Table 2.3). Trap pre-stocking condition did not significantly influence this relationship and was removed from the model via stepwise reduction. Model validation indicated our choice of model was appropriate and the model had a dispersion parameter of 0.95, indicating it was not overdispersed. The output from the model is provided in Table 2.3.

The number of ambient lobster ranged from 5 to 50 (mean ± SD = 21.97 ± 11.24), ambient green crab ranged from 0 to 8 (mean ± SD = 0.27 ± 1.40) and ambient rock crab ranged from 0 to 9 (mean ± SD = 1.70 ± 2.05) (Figure 2.12). Densities of lobster, green crab and rock crab determined by SCUBA surveys ranged from 0.025 to 0.25 lobster/m^2, 0 to 0.04 green crab/m-squared, and 0 to 0.045 rock crab/m^2.

2.4.4 Temporally matched SCUBA and video data

For logistical reasons we were only able to conduct SCUBA surveys for eleven of seventeen deployments. For deployments where video data and SCUBA data were temporally matched (N = 11) we observed significantly more successful entry attempts in the unstocked trap than in either of the crab pre-stocked variants (x^2 = 149.236, df = 2, p = < 2.2e-16; Figure 2.12), which was consistent with our findings for all video deployments together (N = 17). The average number of ambient lobster did not vary significantly around these traps (mean ± 1 SD = unstocked, 23.0 ± 12.57; green crab pre-stock, 21.18 ± 12.80; rock crab pre-stock 21.73 ± 8.97; Figure 2.12).

2.5 Discussion

The goal of this study was to determine whether the presence of green crab inside lobster traps and in the vicinity of deployed traps will influence the trap's lobster catch per unit effort. Our study demonstrates that 1) the presence of crabs can impact the total number of lobster that will attempt to enter the trap as well as the number that do so successfully, 2) both native rock crabs and non-native green crabs reduce the frequency at which lobsters attempt to enter traps, 3) lobster will predate on green crab, rock crab and other lobster inside traps and 4) there is a positive association between lobster catch and ambient lobster density.

2.5.1 Hypothesis 1

Our first hypothesis was that traps pre-stocked with green crab would catch fewer lobster per deployment than unstocked traps, and the camera apparatus would have no detectable impact on catch. In fact, we found that traps pre-stocked with green crab did not catch significantly fewer lobster than unstocked traps, and that the camera apparatus had no observable impact on lobster catch. However, we did find the presence of pre-stocked rock crab markedly reduced lobster catch compared to unstocked traps.

It is unclear why rock-crab pre-stocked traps captured fewer lobster than unstocked traps. Previous studies have attempted to describe the relationship between inter/intraspecific interactions and trap catch rates for lobster and *Cancer* crabs. For example, Miller and Addison (1995), found that in a laboratory environment, catches of green crab and rock crab were reduced in the presence of lobster and those that did enter the trap would avoid the parlour end if lobster were present inside. The number of green crab and rock crab observed around our traps via SCUBA surveys were relatively low as compared to lobster. As a result, we were not able to assess the potential inhibitory effects of lobster inside a trap on green crab and rock crab entrances in the field. Furthermore, Richards et al. (1983), found fewer crabs are caught in traps pre-stocked with more lobster, suggesting a density dependent relationship. Our trials did not manipulate the density of pre-stocked crabs in the kitchen, therefore we were unable to assess whether higher crab densities would have a greater impact on the number of lobster entries. Contrary to our findings, Richards et al. (1983), did not detect an effect of rock crab-stocked traps on lobster catch in their field experiment. However, that pre-stocked individuals in the aforementioned studies were stocked in the parlour of the trap; whereas, we stocked crabs inside the kitchen as opposed to the parlour. We based this decision on observations by Jury et al. (2001), where lobster entry was strongly limited by intraspecific interactions between lobster in the kitchen and those in the entrance. Future research assessing density dependence of this relationship as well as positions of pre-stocked individuals inside the trap would be very useful.

The sizes of captured lobster in our study were similar across all trap pre-stocking conditions and the majority were of sub-legal size. Given that our fieldwork was conducted after closure of the commercial fishery, it is possible that fewer legal sized (> 82.5 mm) lobster were available to be captured. Previous studies have found that the presence of larger individuals inside traps can reduce the catch of smaller individuals for lobster (Watson and Jury, 2013) as well as for green crab and rock crab (Miller and Addison, 1995). Watson and Jury, (2013) suggest that this may be mediated by bait guarding, particularly when smaller individuals attempt to enter the trap. Given that adult lobster are much larger than the pre-stocked green crab and rock crab it is perhaps unsurprising that we did not observe a difference in average lobster size across pre-stocking condition from our catch data.

We did not detect a relationship between the duration of time a trap was soaking in the water and the number of lobster caught across trap pre-stocking condition. However, our video data allowed us to observe and quantify the accumulation of lobster over the first 12 hours of trap deployments. We did not observe more lobster captured at the end of the deployment (24 h) versus at the end of the video observation duration (12 h) for any of the trap pre-stocking conditions. Our results are in general agreement with those of Miller and Rodger (1996), who found traps retrieved more than twice in a 24 hour period captured more lobster than those retrieved only once due to trap saturation.

2.5.2 Hypothesis 2

Our second set of hypotheses pertained to observations derived from *in situ* underwater video. We hypothesized that one (or more) of the following mechanisms were present: 1) green crab invade the trap early in a deployment, deplete the bait, and thereby reduce the numbers of lobster that approach the trap. 2) green crab invade the trap early in a deployment and subsequently block the trap entrances to future lobster entry (i.e. lobster approach, but do not enter). 3) green crab enter traps after lobsters, thus forcing trapped lobsters out of the gear (i.e. green crabs are associated with an increase in exit rates from the trap). The ambient density of green crab was low, and in many videos we saw none at all. As a result, we did not find support for the hypotheses that green crab invade the trap early and either 1) deplete the bait, 2) impede entry and/or 3) force lobster to exit the trap.

We found no support for the bait depletion hypothesis – tethered green crab did not deplete the bait in these traps. However, we did find support for the hypothesis that traps with green crabs had lower rates of lobster entry into traps. Both the number and proportion of successful lobster entries were significantly reduced in traps pre-stocked with green crab, however this effect was not species specific and applied to both invasive green crab and native rock crab. We did not observe any direct interactions of green crabs blocking lobsters, nor did the green crabs appear to interfere with entry attempts. Finally, we did not find an increased lobster exit rate as a result of green crabs in the traps.

Our finding that the proportion of successful lobster entries were reduced in crab-stocked traps aligns with other pre-stocking (Richards et al. 1983) and field studies (Jury et al. 2001) that suggest interactions between lobster inside and outside traps can strongly limit lobster entry and catch. Jury et al. (2001), found that only 11% of lobster entry attempts were successful when the kitchen was occupied versus 64% when the kitchen was vacant. In addition, they note that entry attempts may also be influenced by competition outside the trap where both lobster and crab have been observed competing aggressively for trap entry (Jury et al. 2001). We did not observe any instances of interactions between untethered crabs and lobster during entry attempts. This is likely due to the low density of crabs around traps as observed via our SCUBA surveys. Interestingly, we did not detect any difference between crab pre-stocked traps and unstocked traps for attempts made by small lobster through wire cells and escape slats. This could be attributed to smaller lobster being able to move freely in and out of the traps through these gaps, relatively unimpeded by individuals inside the trap kitchen and parlour.

We found lobster did not take substantially longer to complete a successful entry through the entrance into crab pre-stocked traps compared to unstocked traps. Our video data provided no evidence to suggest that lobster entry was physically impeded by the presence of rock crab or green crab, rather fewer lobster attempted to enter traps where crabs were present. Furthermore, our dive data show that this was not a consequence of lower lobster density around the crab pre-stocked traps.

The underlying mechanism(s) by which pre-stocked crabs reduce lobster catch remains unclear. Though results from various laboratory experiments have suggested that the odor of trapped crab and lobster could repel individuals that might otherwise be attracted to either the bait or the trap as a shelter (Miller and Addison, 1995; Miller, 1978). It is possible that these factors were occurring but we were not able to detect them from our video and SCUBA analyses.

Importantly, we recorded all videos during daylight hours where ambient light was sufficient to make observations. As a result, we were not able to assess interactions that occurred overnight. While previous research suggests that lobster may be more active during the night, a field study by Jury et al. (2001), found no evidence that lobster will enter traps more often during the night. Our data concur with these findings, as we found our catch data (daytime and nighttime) did not significantly differ from our video data, captured during the initial 12 hours of trap deployment (daytime).

Our catch data alone suggested that green crab pre-stocked traps and unstocked traps both captured the same number of lobster, and rock crab pre-stocked traps captured significantly fewer lobster than unstocked traps. However, our video data demonstrated that when traps were pre-stocked with crabs, successful entries as well as entry attempts of lobster were significantly reduced. This disparity between catch and video data represents a difference between coarse scale catch data, and fine scale video data. Direct observation with underwater video allowed us to quantify the total number of entry attempts, failed attempts, exits from the trap as well as aggression and predation events. Our trap deployments collated 85 observations of catch data and recorded 452 hours of underwater video data which was analysed to produce around 10,000 individual observations. This provides a compelling difference between the breadth of information we can glean from 85 observations of catch data as compared to 452 hours of in-depth video analysis.

Previous laboratory studies have demonstrated that predation is possible between lobster and green crab (Goldstein et al. 2017). Our study is the first to provide evidence of this dynamic occurring inside lobster traps observed in the field using long duration underwater video. In some instances, pre-stocked crabs were consumed in preference to a full bait bag. It is important to note that crabs in our study were tethered inside traps and were not able to flee from aggressors, potentially forcing these interactions. In general, this dominance dynamic aligns with a large body of literature on agonistic behaviours in crustaceans showing that the larger animal typically dominates in aggressive contests (Dingle 1983; Hyatt, 1983; Rossong et al. 2006). Interestingly, our underwater video also enabled us to observe multiple events of cannibalism where trapped adult lobster were dismembered and consumed by other lobster in the parlour of the trap. In previous laboratory trials Haarr and Rochette, (2012) found that at high densities juvenile lobster would consume conspecifics. However, they did not observe juvenile lobster predating on green crab.

2.5.3 Hypothesis 3

Our final hypothesis was that green crab-induced reductions of lobster catch would be stronger for gear deployments where the ambient green crab density was higher. Due to the low ambient density of green crab observed via our SCUBA surveys we found no support for this hypothesis.

The results from our SCUBA surveys did, however, suggest there is a positive relationship between lobster catch and the number of lobster around the traps, this is consistent with a field study by Watson and Jury, (2013). We did not detect any difference in the mean number of lobster around each trap type based on our diver-based density estimates. These findings bolster the results from our underwater video which suggested that the number of successful attempts vary markedly according to the presence of pre-stocked crabs inside lobster traps. Our SCUBA data confirmed there were comparable densities of lobster around each trap, eliminating variations in lobster abundance as a contributing factor influencing the differences in lobster entry attempts and successes according to trap pre-stocking condition.

SCUBA surveys were an effective method for estimating lobster and crab density (Tremblay et al. 2005). However, this approach is subject to biases including habitat type, diver disturbance as well as the fact that dives were restricted to daylight hours (Tremblay and Smith, 2001). Most of our survey sites were characterized by either sand or small cobble, making it relatively easy to detect crabs and lobster along transects. We were unable to statistically test the effect of diver disturbance on transect data.

While we did not observe many green crab along transects during the summer of 2016, when we went back the following summer we observed (via snorkeling) far more green crab at these same sites than were there previously (pers. obs., unpublished data, 2017).

With the recent increase of invasive green crab populations invading colder marine habitats such as those in Newfoundland, the need to understand how they will impact native species as well as coastal fisheries is becoming increasingly urgent. Importantly, at the densities we investigated, we found no evidence to suggest that there was a green crab-specific effect. Few field studies have assessed the magnitude of the direct and indirect impacts of native crabs compared to non-native crab species (Howard et al. 2017). In their global meta-analysis, Howard et al. (2017) found non-native crabs did not reduce prey abundance via direct consumption any more than native crabs. More research into the direct interactions between native and non-native species will be crucial to the development of effective management initiatives.

Though we did not detect a species specific effect between native rock crab and non-native green crab, one cause for concern is that in heavily invaded systems green crab have been observed readily accessing and being captured by lobster traps (Goldstein et al. 2017). In the Great Bay Estuary, New Hampshire, Goldstein et al. (2017), captured ~8.5 times more green crab than lobster. If green crab access traps, our results suggest that the number and proportion of lobster that enter the trap may be reduced, and that this reduction is not related to any unique quality of the invader but rather the sheer abundance of green crab relative to native species.

In the case of green crab, the magnitude of the invasion surpasses our ability to completely remove them from invaded systems. However, it may be possible to suppress populations to a point where they no longer elicit negative ecological effects (Green et al. 2014). Green et al. (2014) suggest that this can be accomplished through identifying a population threshold based on the mechanisms by which the invasive species affects native communities, and creating removal targets based on this threshold. In this way, removal targets are tailored to ameliorate the specific ecological effects of the invader. This will aid managers in making decisions about how to allocate resources to address the removal and control of invasive green crab in priority habitats, such as Fortune Bay, Newfoundland.

2.5.4 Conclusions

Our findings have shown that the presence of crabs inside lobster traps can influence lobster catch. This is a result of fewer lobster both attempting entry as well as successfully completing entry in crab pre-stocked traps. Importantly, this effect was not specific to green crab, but both invasive green crab and native rock crab. Using SCUBA survey data we were able to determine that the difference in total entry attempts as well as the proportion of entry successes was not simply a result of higher lobster density around unstocked traps as compared to crab pre-stocked stocked traps. If green crab establish in Fortune Bay in high densities and abundances similar to those observed in Placentia Bay it is possible that they will more readily overlap with lobster in traps. This enhanced overlap between lobster and green crab inside traps has the potential to decrease the number of lobster that enter lobster traps. Future research into estimating targets for invasive green crab removal would be very useful in order to aid mitigation initiatives. It would also be useful to determine both the environmental and trapping densities of green crab that effect lobster catches, as well as the extent that environmental densities of green crab, rock crab and lobster co-vary.

Tables

Table 2.1 Model output from equation 1. Estimated regression parameters, standard errors, z-values and P-values.

	Estimate	Std. error	z value	P-value
Intercept	1.4476	0.1770	8.181	2.82e-16
Green crab pre-stock	-0.3124	0.1684	-1.855	0.0636
Rock crab pre-stock	-0.4364	0.1747	-2.499	0.0125
Standard trap	-0.2247	0.1396	-1.610	0.1074

Table 2.2 Model output from equation 2. Estimated regression parameters, standard errors, z-values and P-values.

	Estimate	Std. error	z value	P-value
Intercept	1.4447	0.1916	7.541	4.66e-14
Green crab pre-stock	-0.2908	0.2064	-1.409	0.1589
Rock crab pre-stock	-0.4155	0.2118	-1.962	0.0498
Standard trap	-0.2278	0.1735	-1.313	0.1891

Table 2.3 Model output from equation 3.Estimated regression parameters, standard errors, z-values and P-values.

	Estimate	Std. error	z value	P-value
Intercept	1.105111	0.189895	5.820	5.9e-09
Ambient Lobster	0.016014	0.007093	2.258	0.024

Supplementary Tables

Supplementary Table 2.1. Summary of deployments and SCUBA surveys. Blank values in the SCUBA columns indicate deployments where dive surveys were not conducted.

Date	Deployment	Site	Pre-stocking condition	Lobster catch	Green crab catch	Rock crab catch	Ambient lobster density (SCUBA)	Ambient green crab density (SCUBA)	Ambient rock crab density (SCUBA)
7/4/2016	1	Little Harbour East	GC	2	0	0			
7/4/2016	1	Little Harbour East	RC	3	0	0			
7/4/2016	1	Little Harbour East	Unstocked	1	0	0			
7/4/2016	1	Little Harbour East	No cam-Unstocked	4	0	0			
7/4/2016	1	Little Harbour East	No Cam-Unstocked	1	0	0			
7/5/2016	2	Little Harbour East	Unstocked	1	0	0	5	0	0
7/5/2016	2	Little Harbour East	RC	4	0	0	5	0	0
7/5/2016	2	Little Harbour East	GC	4	0	0	13	0	0
7/5/2016	2	Little Harbour East	No Cam-Unstocked	2	0	0			

7/5/2016	2	Little Harbour East	No Cam-Unstocked	1	0	0			
7/6/2016	3	Little Harbour East	GC	3	0	0	6	8	1
7/6/2016	3	Little Harbour East	RC	2	0	0	18	0	5
7/6/2016	3	Little Harbour East	Unstocked	2	0	0	20	1	5
7/6/2016	3	Little Harbour East	No Cam-Unstocked	2	0	0			
7/6/2016	3	Little Harbour East	No Cam-Unstocked	2	0	0			
7/7/2016	4	Little Harbour East	GC	7	0	0	48	0	5
7/7/2016	4	Little Harbour East	RC	7	0	0	39	0	3
7/7/2016	4	Little Harbour East	Unstocked	4	0	0	50	0	9
7/7/2016	4	Little Harbour East	No Cam-Unstocked	8	0	0			
7/7/2016	4	Little Harbour East	No Cam-Unstocked	2	0	0			

7/18/2016	5	Little Bay East	Unstocked	0	0	0
7/18/2016	5	Little Bay East	RC	1	0	0
7/18/2016	5	Little Bay East	No Cam-Unstocked	1	0	0
7/18/2016	5	Little Bay East	GC	0	0	0
7/18/2016	5	Little Bay East	No Cam-Unstocked	0	5	2
7/19/2016	6	Little Bay East	RC	0	0	0
7/19/2016	6	Little Bay East	Unstocked	1	0	0
7/19/2016	6	Little Bay East	No Cam-Unstocked	0	0	0
7/19/2016	6	Little Bay East	GC	0	1	1
7/19/2016	6	Little Bay East	No Cam-Unstocked	1	0	0
8/8/2016	7	Little Harbour East	GC	0	0	0

8/8/2016	7	Little Harbour East	RC	3	0	0			
8/8/2016	7	Little Harbour East	Unstocked	11	0	0			
8/8/2016	7	Little Harbour East	No Cam-Unstocked	4	0	0			
8/8/2016	7	Little Harbour East	No Cam-Unstocked	8	0	0			
8/9/2016	8	Little Harbour East	RC	3	0	0	21	0	0
8/9/2016	8	Little Harbour East	Unstocked	7	0	0	14	0	0
8/9/2016	8	Little Harbour East	GC	4	0	0	7	0	1
8/9/2016	8	Little Harbour East	No Cam-Unstocked	2	0	0			
8/9/2016	8	Little Harbour East	No Cam-Unstocked	6	0	0			
8/10/2016	9	Little Harbour East	Unstocked	2	0	0	14	0	1
8/10/2016	9	Little Harbour East	RC	3	0	0	16	0	0

8/10/2016	9	Little Harbour East	GC	4	0	0	36	0	3
8/10/2016	9	Little Harbour East	No Cam-Unstocked	1	0	0			
8/10/2016	9	Little Harbour East	No Cam-Unstocked	3	0	0			
8/11/2016	10	Little Harbour East	GC	7	0	0	25	0	1
8/11/2016	10	Little Harbour East	RC	5	0	0	16	0	3
8/11/2016	10	Little Harbour East	Unstocked	7	0	0	16	0	3
8/11/2016	10	Little Harbour East	No Cam-Unstocked	2	0	0			
8/11/2016	10	Little Harbour East	No Cam-Unstocked	1	0	0			
8/22/2016	11	Little Harbour East	GC	6	0	0			
8/22/2016	11	Little Harbour East	RC	3	0	0			
8/22/2016	11	Little Harbour East	Unstocked	5	0	0			

8/22/2016	11	Little Harbour East	No Cam-Unstocked	7	0	0			
8/22/2016	11	Little Harbour East	No Cam-Unstocked	5	0	0			
8/23/2016	12	Little Harbour East	Unstocked	10	0	0	33	0	3
8/23/2016	12	Little Harbour East	RC	1	0	0	26	0	0
8/23/2016	12	Little Harbour East	GC	5	0	0	20	0	1
8/23/2016	12	Little Harbour East	No Cam-Unstocked	1	0	0			
8/23/2016	12	Little Harbour East	No Cam-Unstocked	7	0	0			
8/24/2016	13	Little Harbour East	Unstocked	7	0	0	24	0	1
8/24/2016	13	Little Harbour East	RC	3	0	0	32	0	0
8/24/2016	13	Little Harbour East	GC	2	0	0	29	0	3
8/24/2016	13	Little Harbour East	No Cam-Unstocked	18	0	0			

8/24/2016	13	Little Harbour East	No Cam-Unstocked	4	0	0			
8/25/2016	14	Little Harbour East	GC	4	0	0	15	0	2
8/25/2016	14	Little Harbour East	RC	1	0	0	17	0	1
8/25/2016	14	Little Harbour East	Unstocked	6	0	0	17	0	0
8/25/2016	14	Little Harbour East	No Cam-Unstocked	3	0	0			
8/25/2016	14	Little Harbour East	No Cam-Unstocked	6	0	0			
9/6/2016	15	Little Harbour East	No Cam-Unstocked	4	0	0			
9/6/2016	15	Little Harbour East	GC	4	0	0			
9/6/2016	15	Little Harbour East	RC	6	0	0			
9/6/2016	15	Little Harbour East	Unstocked	5	0	0			
9/6/2016	15	Little Harbour East	No Cam-Unstocked	8	0	0			

9/7/2016	16	Little Harbour East	GC	5	0	0	22	0	0
9/7/2016	16	Little Harbour East	RC	3	0	0	18	0	1
9/7/2016	16	Little Harbour East	Unstocked	6	0	0	24	0	0
9/7/2016	16	Little Harbour East	No Cam-Unstocked	5	0	0			
9/7/2016	16	Little Harbour East	No Cam-Unstocked	5	0	0			
9/8/2016	17	Little Harbour East	Unstocked	7	0	0	36	0	2
9/8/2016	17	Little Harbour East	GC	3	0	0	12	0	2
9/8/2016	17	Little Harbour East	RC	5	0	0	21	0	3
9/8/2016	17	Little Harbour East	No Cam-Unstocked	5	0	0			
9/8/2016	17	Little Harbour East	No Cam-Unstocked	2	0	0			

Supplementary Table 2.2. Summary of all green crab and rock crab entry attempts, successful entries, and exits from 452 hours of underwater video analyzed. Summarized by deployment and trap pre-stocking condition.

Deployment	Pre-stocking condition	Species	Total entry attempts	Total successful entries	Total exits
3	GC pre-stocked	GC	17	13	11
5	GC pre-stocked	GC	7	6	3
5	GC pre-stocked	RC	6	6	5
5	RC pre-stocked	RC	2	2	1
5	Unstocked	GC	1	1	1
6	GC pre-stocked	GC	2	1	0
6	GC pre-stocked	RC	1	1	0
6	RC pre-stocked	GC	10	4	3
6	RC pre-stocked	RC	3	2	2
6	Unstocked	GC	8	2	1
6	Unstocked	RC	4	4	4
11	RC pre-stocked	RC	1	1	1
17	GC pre-stocked	RC	1	1	0

Figures

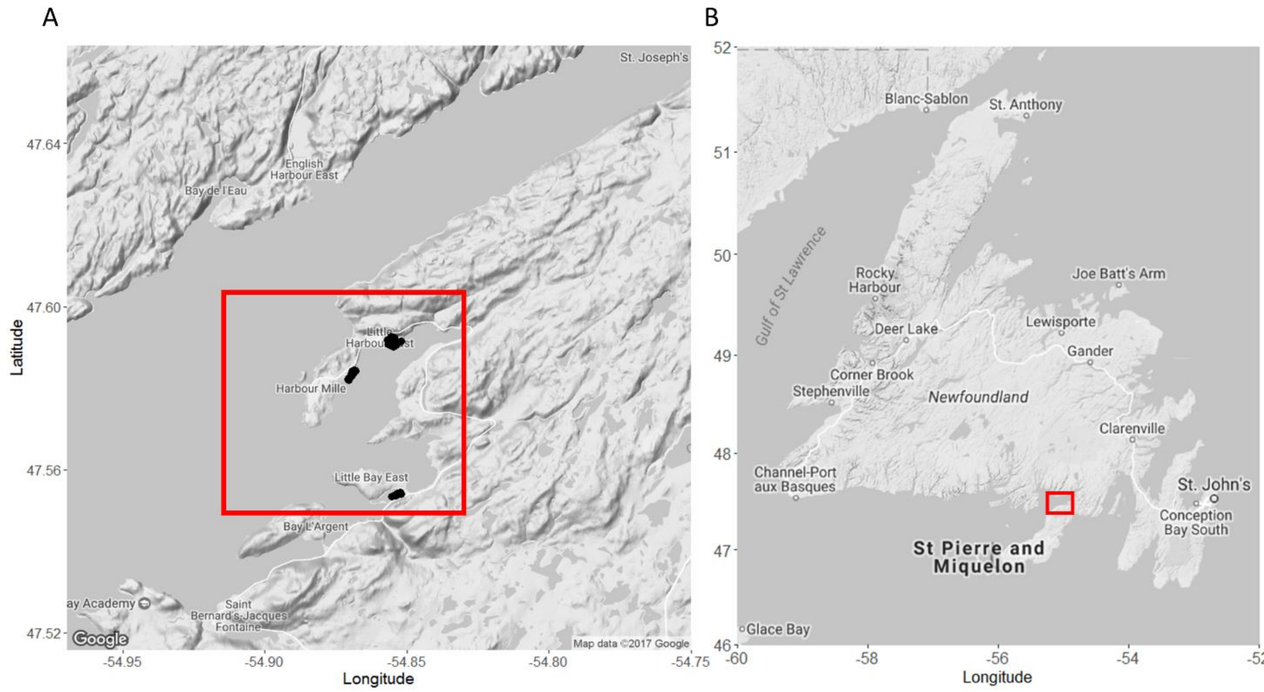

Figure 2.1 (A) Map of our study sites in Little Harbour East and Little Bay East, Fortune Bay, off the southern coast of Newfoundland. Black points indicate where we deployed our traps. Red squares indicate the location of our study sites relative to the rest of Newfoundland (B).

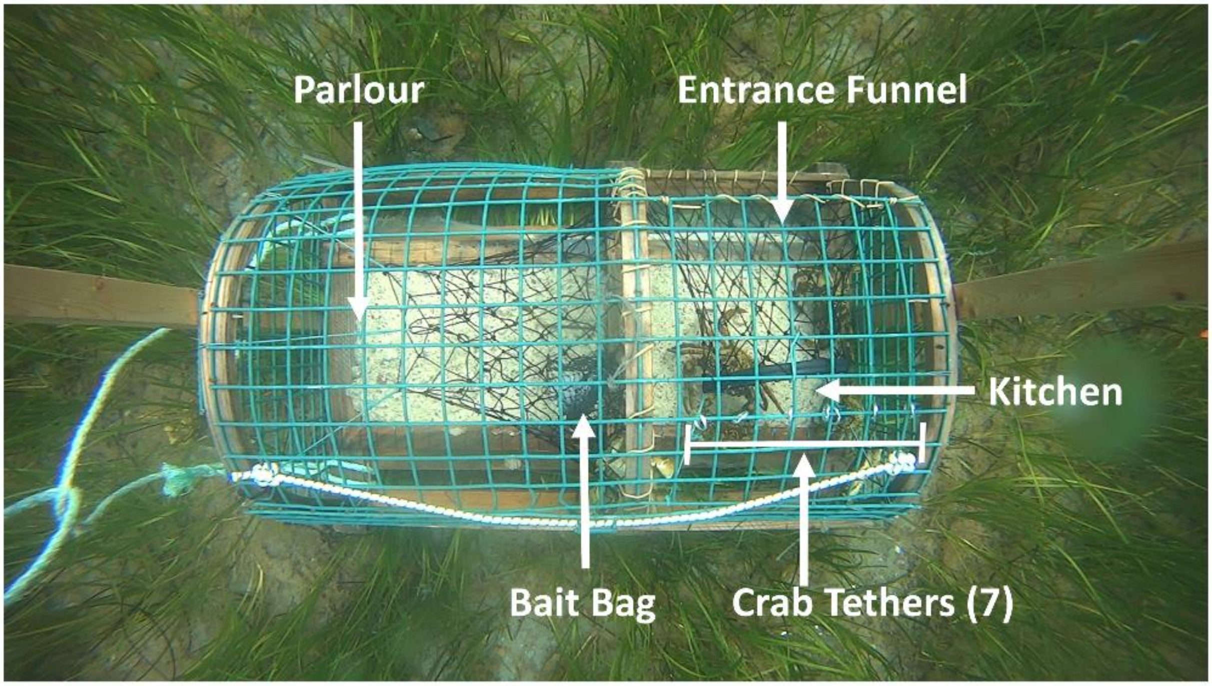

Figure 2.2 Top-down view of a green crab pre-stocked camera trap. The mesh entrance funnel leads into the kitchen compartment where the bait bag is stored and where 7 crabs were tethered using fishing line tied to split metal rings that were attached to wire cells on the top of the trap. The parlour refers to the area where lobsters are retained.

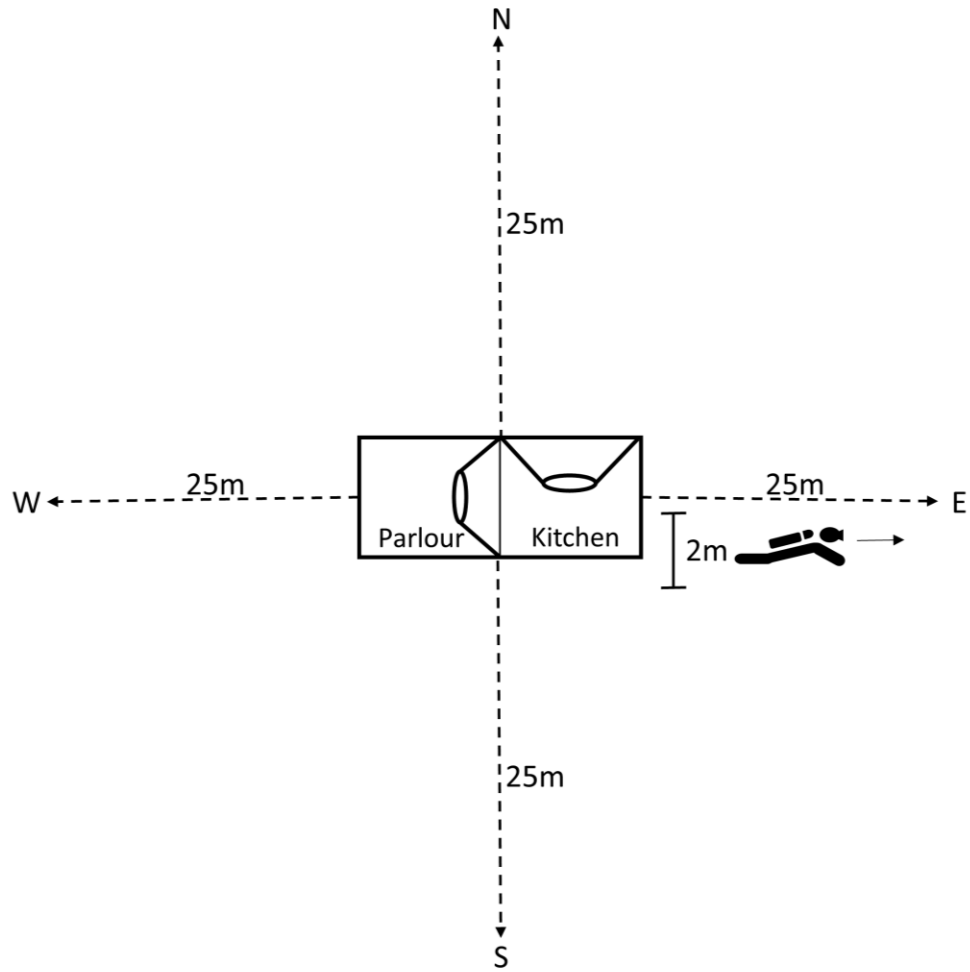

Figure 2.3 Top view of SCUBA transects conducted on camera traps. Dotted lines indicate the 25m transects, oriented North, South, West and East of the camera trap (shown in the centre of the image). The 2m marking indicates the area in which divers recorded counts of green crab, lobster and rock crab.

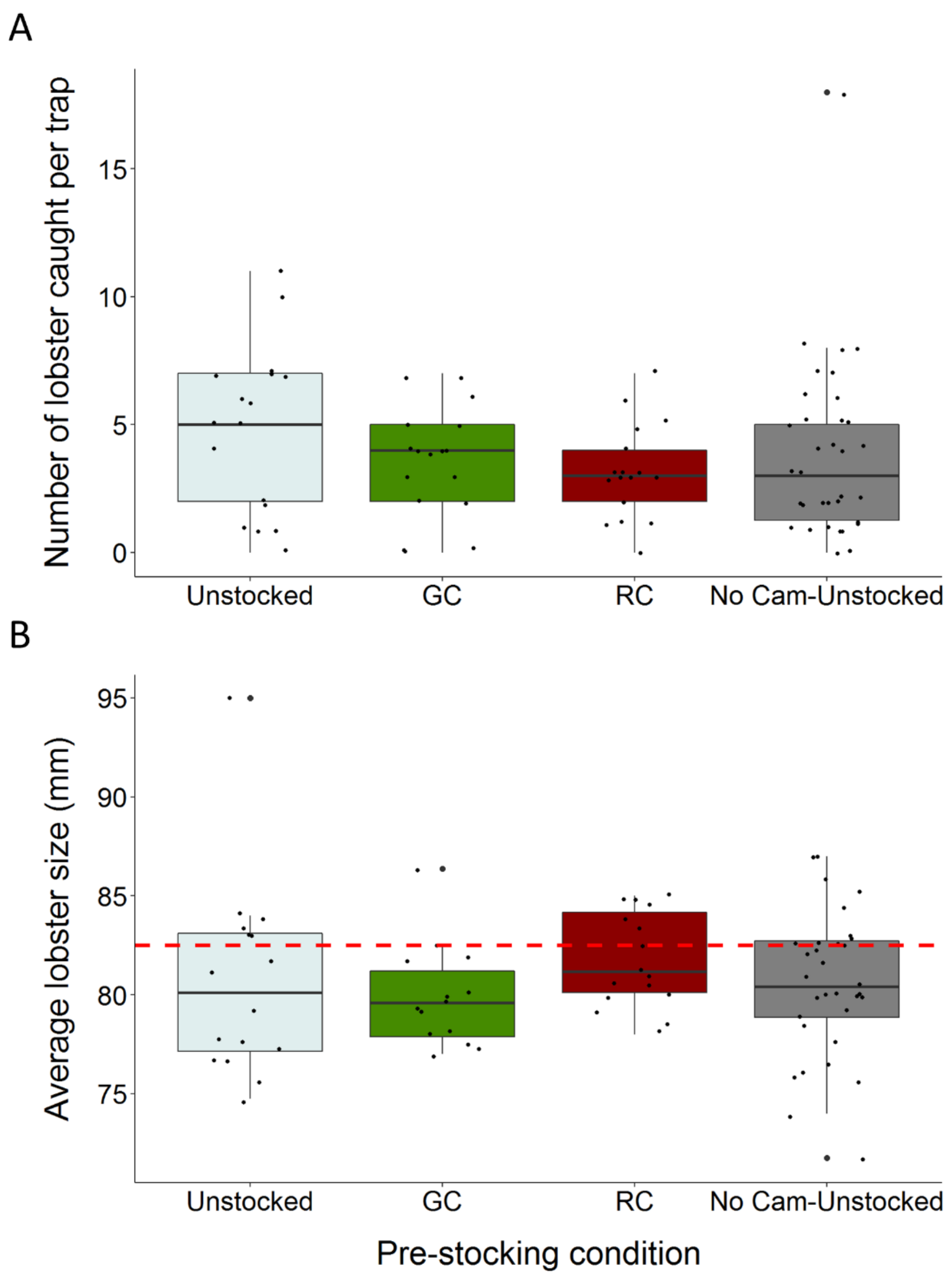

Figure 2.4 Boxplots comparing (A) the distributions of total lobster catch according to trap pre-stocking condition (B) the distributions of average lobster size (carapace length) across trap pre-stocking conditions (the dotted red line indicates the minimum legal size of 82.5 mm carapace length). Each black dot represents a single observation.

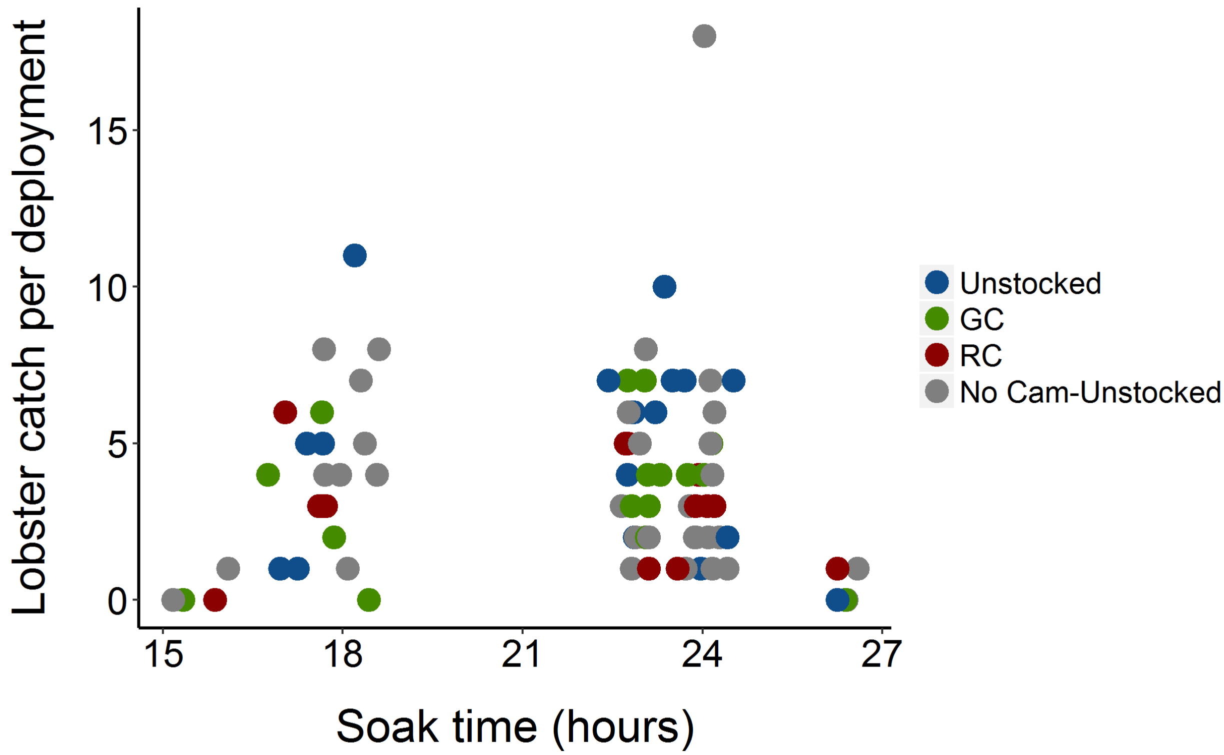

Figure 2.5 The number of lobster caught in relation to the time the trap was in the water for each pre-stocking condition.

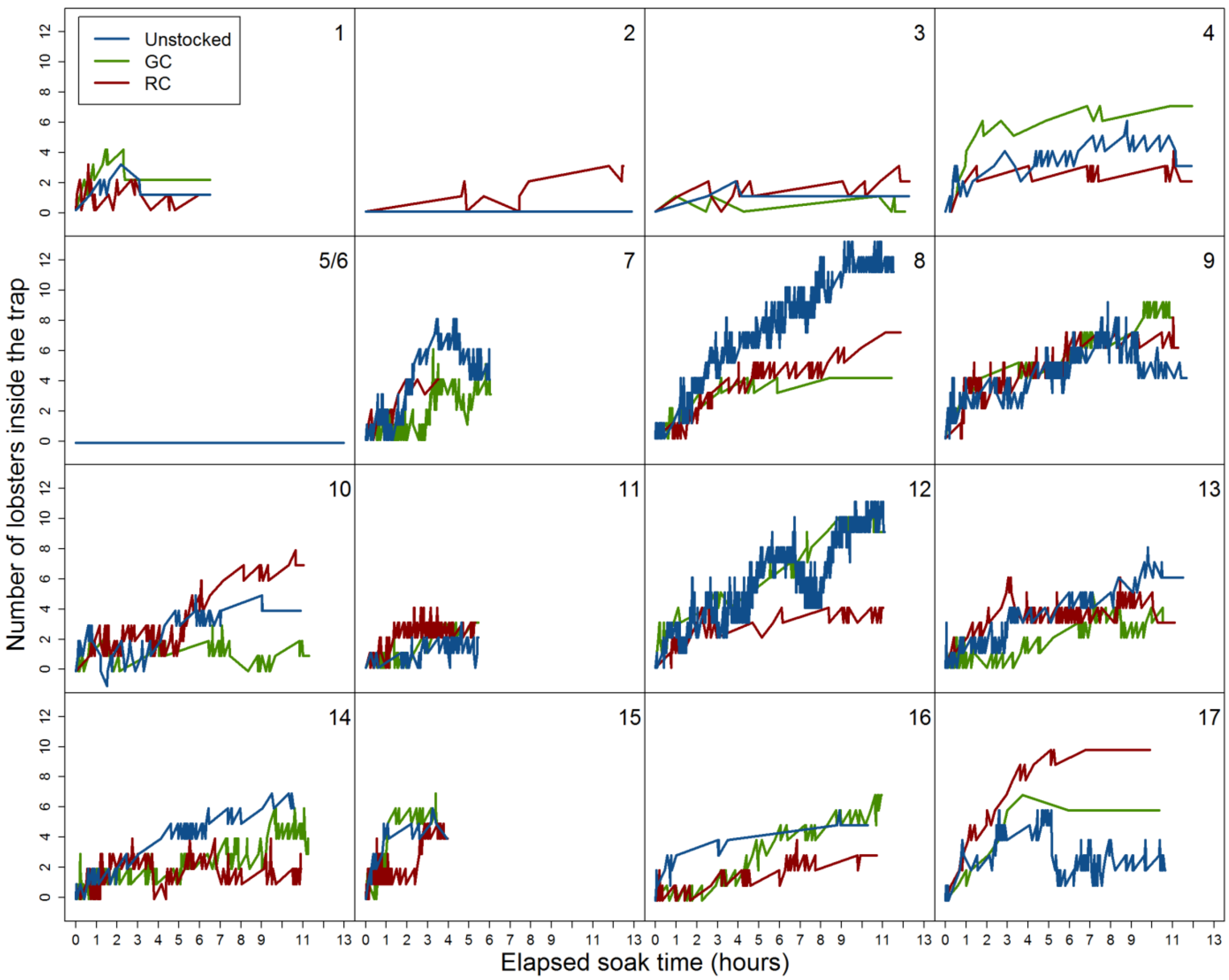

Figure 2.6 Comparison of lobster accumulation over the elapsed soak time for all entries and exits. Each coloured line represents pre-stocking condition of traps. Numbers at the top right of each plot represents the deployment.

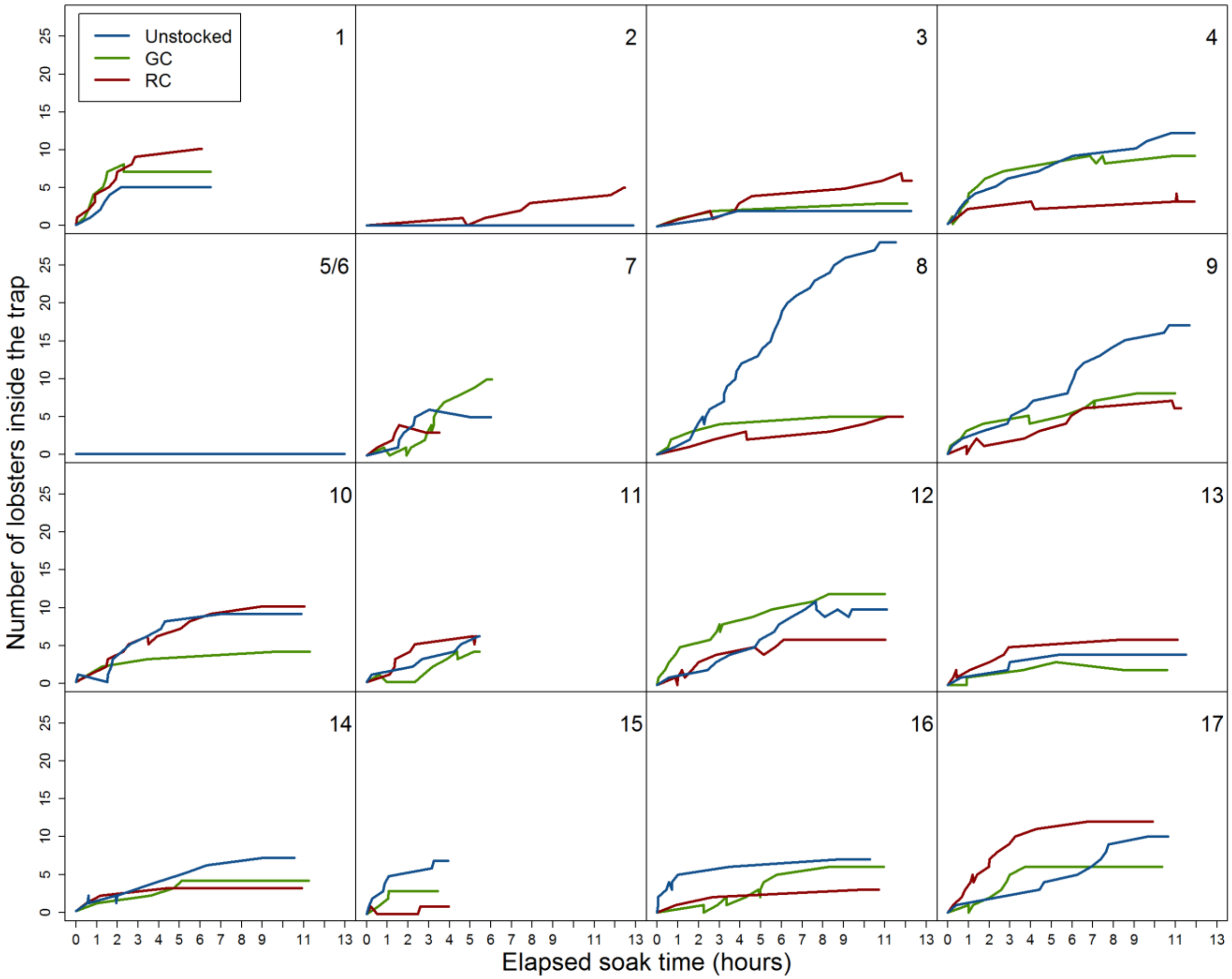

Figure 2.7 Comparison of lobster accumulation over the elapsed soak time for entries and exits through the trap entrance only (i.e. primarily large-bodied lobsters). Each coloured line represents trap pre-stocking condition. Numbers at the top right of each plot represents the deployment.

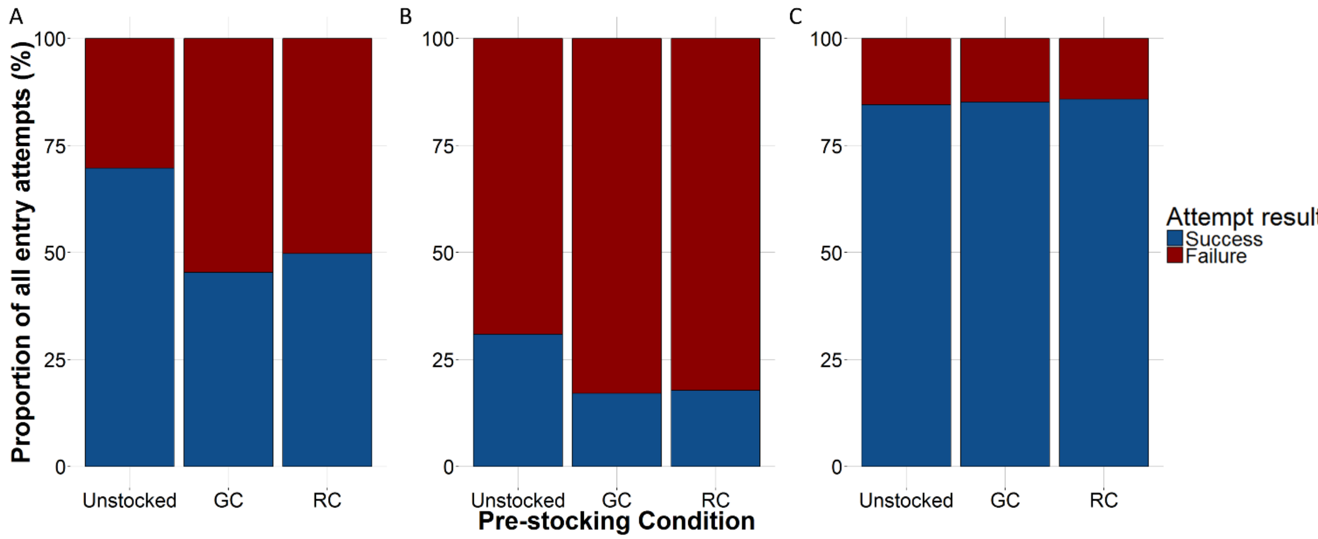

Figure 2.8 The proportion of lobster entry attempts that were either successful (blue) or failed (red) according to trap pre-stocking condition for (A) all entry attempts, (B) entry attempts through the trap entrance only (i.e. primarily large-bodied lobster), (C) entry attempts through the wire cells or escape slats only (i.e. primarily small-bodied lobsters).

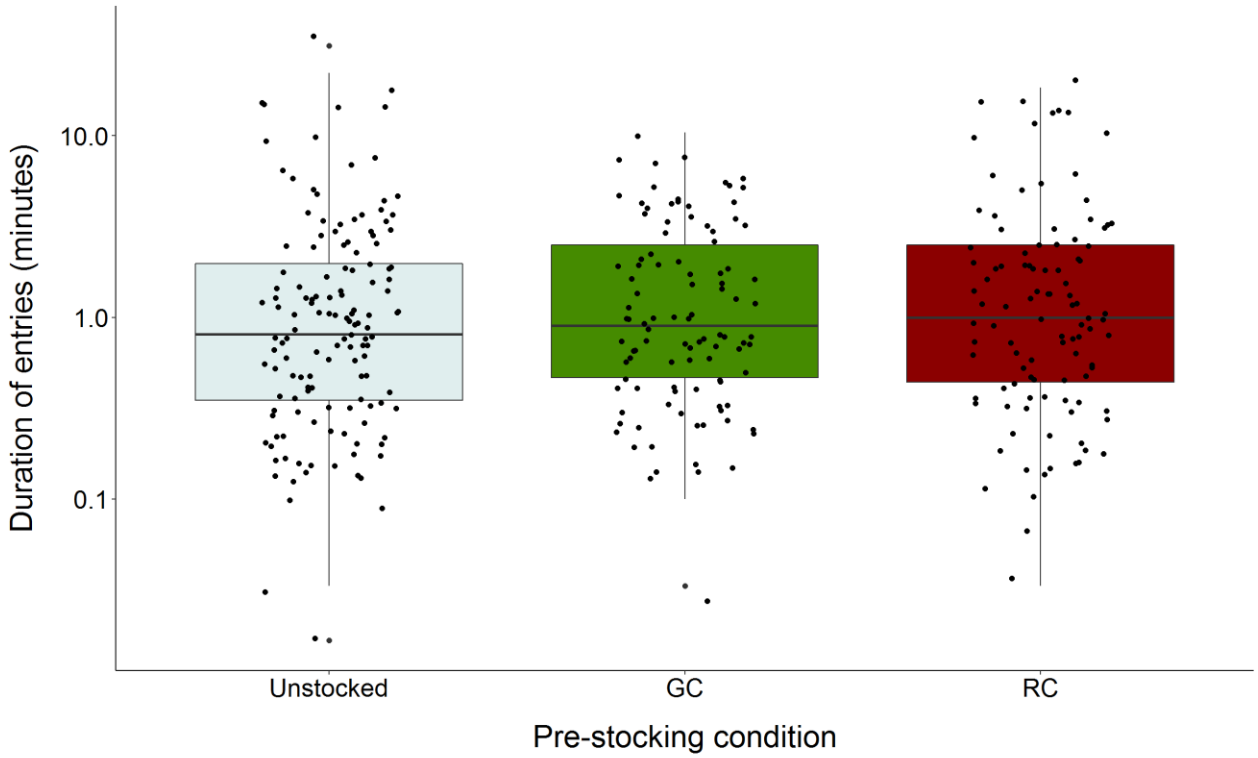

Figure 2.9 Boxplot of lobster entry time (log scale) for successful attempts through the entrance across trap pre-stocking condition. The horizontal lines indicate the medians for each trap pre-stocking condition. Each dot represents a single entry attempt.

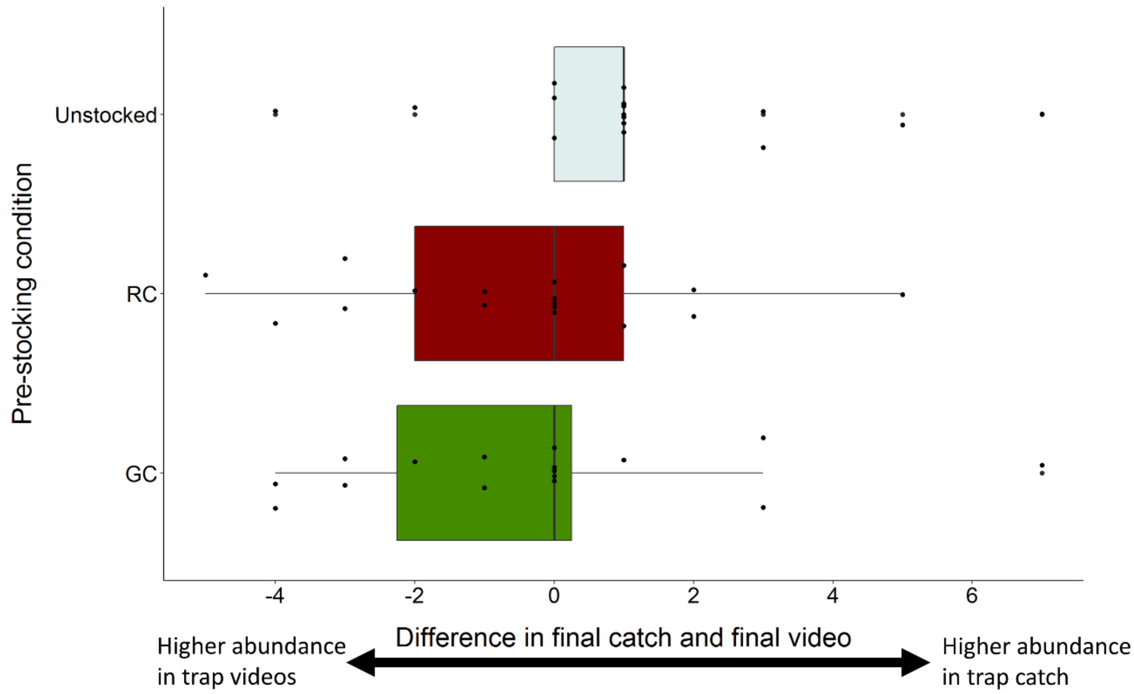

Figure 2.10 Boxplot illustrating the difference between the number of lobster inside the trap at the end of the soak period compared to the number of lobster inside the trap at the end of the video observation for each trap pre-stocking condition.

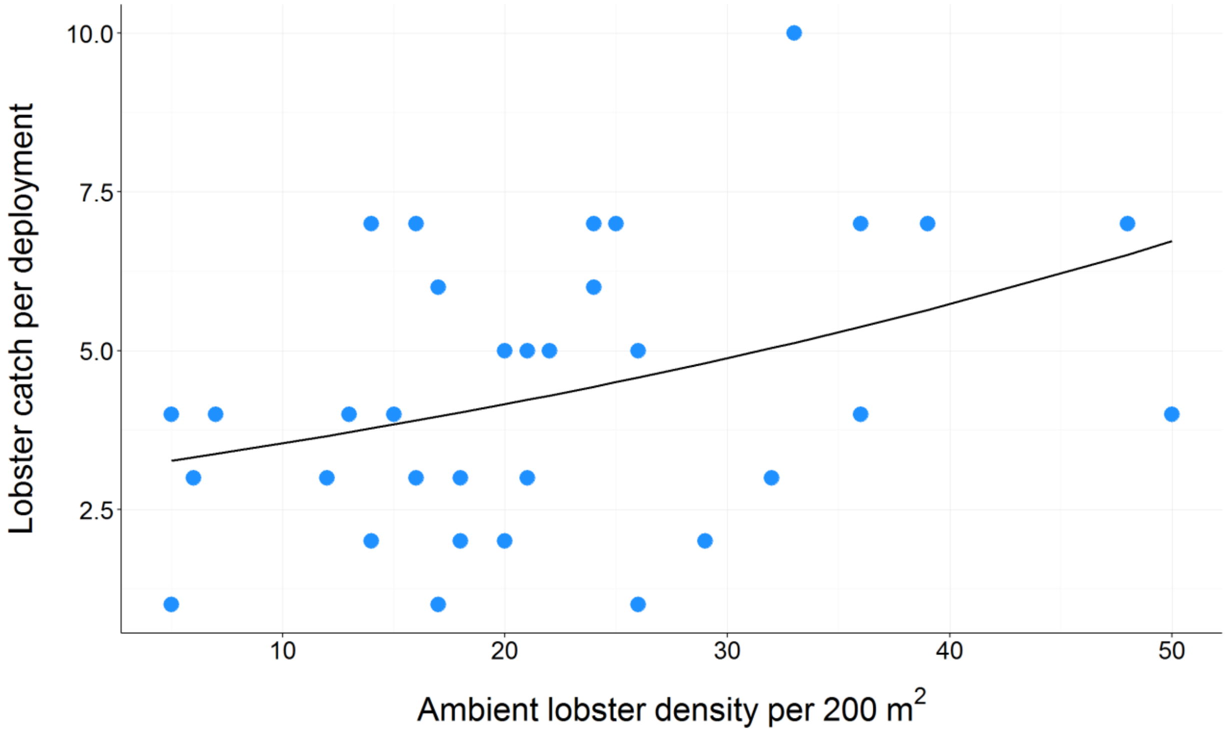

Figure 2.11 The relationship between lobster catch per deployment and ambient lobster density. The black line indicates the fitted Poisson generalized linear mixed-effects model.

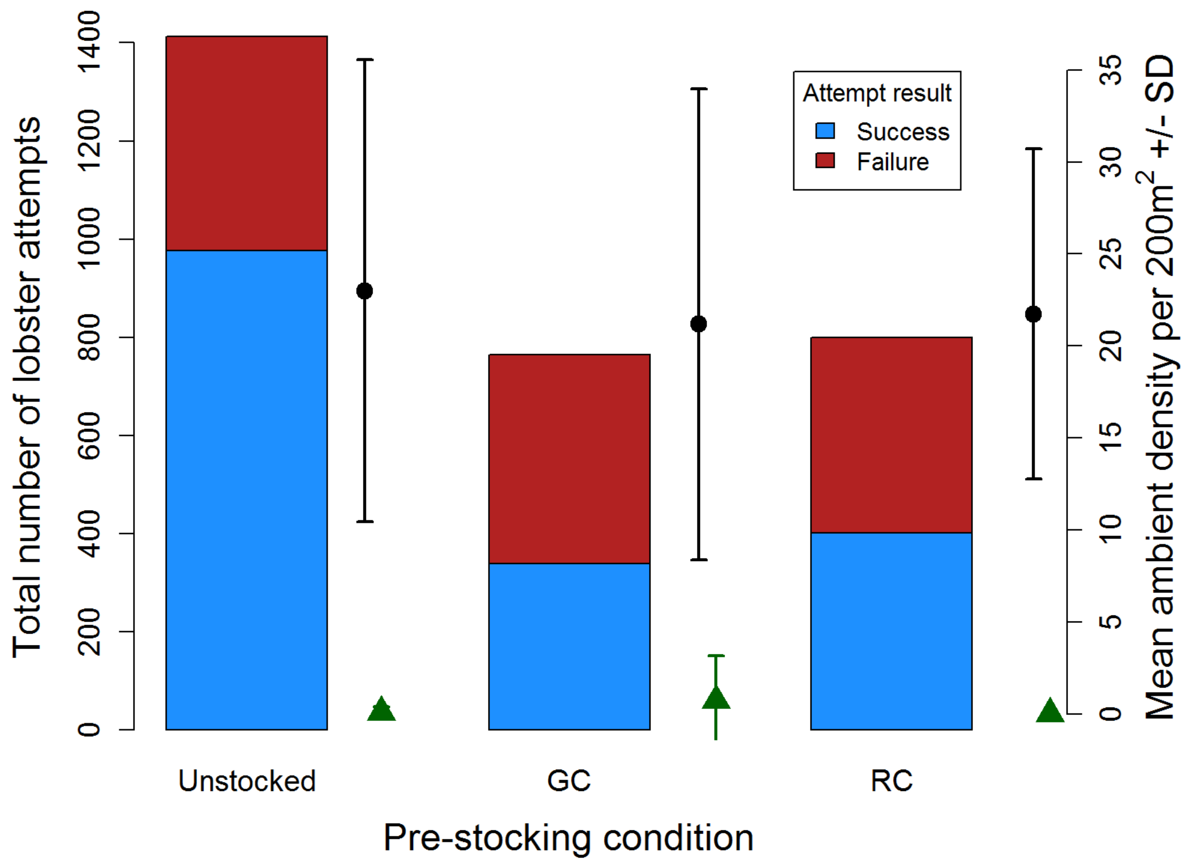

Figure 2.12 Total number of successful (blue) and failed (red) lobster entry attempts observed across trap pre-stocking condition for deployments with both video and SCUBA data (N = 11). The black points and lines indicate mean ambient lobster density ± 1 SD surveyed around each trap pre-stocking condition. The green triangles and lines indicate mean ambient green crab density ± 1 SD surveyed around each trap pre-stocking condition m^2

Summary

Green crab abundance in many invaded habitats across the Atlantic coast has swiftly increased (DFO, 2011). This, coupled with the impossibility of eradication, highlights the importance of employing ecologically effective techniques to suppress invasive green crab populations below specific target levels predicted to cause negative ecological effects. A study by Green et al. 2014 developed and tested removal targets for the control of invasive Indo-Pacific lionfish (*Pterois volitans* and *P. miles*) on Western Atlantic coral reefs. They found that native prey fish biomass increased by 50-70% on reefs where lionfish were kept below threshold densities. Their work was the first to demonstrate that for persistent invasions, suppressing invasive species below densities that cause harm to native ecosystems can have a similar effect to achieving complete eradication on a local scale.

Future research should be aimed towards predicting threshold densities of green crab beyond which lobster catch rates may decline. If control programs are informed by relevant target thresholds, managers will be able to make efficient use of removal resources to prevent negative ecological effects of invasive green crab in priority habitats.

In addition, with greater understanding of factors that limit the distribution of native crab species we may be better equipped to identify priority areas that are most vulnerable to invasion by green crab, and allocate resources towards effective mitigation initiatives. Researchers in California and Chesepeake Bay (DeRivera et al., 2005; Jensen et al., 2007) found that native crustaceans could act as a mitigating factor to control the spread of green crab. DeRivera et al., (2005) demonstrated via trapping surveys and tethering experiments that green crab abundance was significantly reduced at sites and depths occupied by a native crustacean species *C. sapidus.* A similar study by Jensen et al., (2007) in central California found a comparable trend that native *Cancer* spp. crab could limit the distribution and habitat use of green crab. However, Jensen et al., (2007) suggest this may only occur in areas where they overlap with native crab species and that biotic resistance may only partially control the spread of green crab. Importantly, green crab are able to exploit habitats that native crab species are unable to tolerate, withstanding wide temperature (Carlton and Cohen, 2003) and salinity extremes (Broekhuysen, 1936) as well as desiccation (Cohen et al., 1995). The importance of native crab species as biological controls also highlights the need to manage recreational and commercial fisheries associated with native crab species. Future research directed towards understanding appropriate target thresholds as well as removal timelines relative to the thresholds for impact would be greatly beneficial.

Previous studies have used catch data coupled with laboratory trials to assess the effects of behavioural interactions among species on lobster catch. Our study describes the relationship between lobster and green crab inside and around fishing gear in the field, and is the first to reveal a relationship between the presence of crabs inside a trap and subsequent lobster entry attempts from *in situ* empirical data using underwater video, pre-stocking techniques, and SCUBA surveys.

Our research highlights how underwater video can serve as a powerful tool for field-based studies. The benefits of using underwater video to study these interactions *in situ* are that it allows us to increase our observation time, maximizing behavioural information, and enabling us to quantitatively assess lobster capture efficiency far beyond what catch data alone reveals.

We believe that this research reveals important behavioural dynamics at the trap level between lobster and both native and invasive crab species and offers valuable insights for productive directions for future research into the relationship between green crab and lobster.

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