

EVALUATING THE IMPACTS OF MARINE PROTECTED AREAS ON  
ECOLOGICAL PROCESSES IN BENTHIC FISHERIES: APPLYING  
ECOSYSTEM-BASED STRATEGIES TO FISHERIES MANAGEMENT

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EVALUATING THE IMPACTS OF MARINE PROTECTED AREAS ON  
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Marine protected areas (MPAs) are increasingly employed worldwide to manage and conserve marine ecosystem services such as fisheries, coastal protection, habitat restoration, biodiversity conservation and tourism. They are frequently used as a place-based approach with the aim of conserving fishery resources by restricting fishing to specific zones. MPAs are particularly useful for managing species that are not highly migratory since these species' habitats can be restricted to ranges within zoning boundaries. For example, benthic communities and many invertebrate fisheries can be managed by the use of MPAs because their habitat ranges can be delineated and zoned for protection or exploitation. In this work, I have researched ecological interactions in the benthic community of MPAs and evaluated governance strategies used to promote compliance with MPA regulations. Enforcement of MPAs remains one of the key factors in ensuring sustainable resource use for some fisheries, though enforcement mechanisms leading to successful outcomes remain poorly understood worldwide. As a result, it is necessary to consider how different governance strategies used to encourage compliance with MPA regulations may best sustain fishery resources. In chapter one, I have analyzed different strategies used to promote compliance with regulations on ecological indicators of condition in the

Greater Caribbean region. I found that the use of both penalties and incentives to promote compliance may help form successful governance strategies. I also have examined ecological relationships affected by the presence of MPAs. In chapter two I evaluate the distribution of an invasive tunicate, its interaction with the Atlantic sea scallop and the impact of the protected area as compared to open areas on this interaction. In chapter three I evaluate how the invasive tunicate interacts with other species of the invertebrate community and how these interactions are altered by the protected area and the presence of fishing. This work enhances our understanding of marine management, through an analysis of MPA governance and ecological interactions shaped by MPAs. Understanding both the governance and ecological aspects of MPAs provides a holistic framework for understanding their utility for marine conservation and management.

## BIOGRAPHICAL SKETCH

Katherine Kaplan was born in New Rochelle, NY on May 21<sup>st</sup>, 1986. She grew up in New Rochelle and attended New Rochelle High School, where she graduated from in 2004. She then attended Grinnell College in Grinnell, Iowa for her undergraduate studies majoring in Biology with a concentration in Global Development Studies. She graduated from Grinnell College in December of 2008. During college she worked as an Emergency Medical Technician at the Midwest Ambulance company in Grinnell, IA. After college her first job was working on the National Children's study in New York City and then in a genetics lab processing DNA samples at the Feinstein Institute for Biomedical Research, a branch of Northshore University hospital on Long Island in Manhasset, NY. After that she moved to teach English in the Galapagos Islands at the Galapagos Academic Institute of the Arts and Sciences (GAIAS), a satellite campus of Universidad San Francisco de Quito (USFQ). During this time she became involved with a fish biodiversity monitoring project through the Galapagos National Park. Through this experience she became interested in marine ecology and joined the Master's of Science program at Universidad San Francisco de Quito in 2011 in Quito, Ecuador working with researchers she had met at GAIAS-USFQ. She completed her Master's degree in Ecology in August of 2012. Her Master's thesis is entitled: "Concepts of vulnerability as drivers of conservation priorities: an applied study of fish communities in the Galapagos Marine Reserve". She decided to continue studying in the field and began to pursue her Ph.D. under the direction of Patrick Sullivan in August of 2012 in the Department of Natural Resources at Cornell University. She has taught as a teaching assistant to support her graduate studies in the following courses: Introduction to Ecology, Society and Natural Resources, Wetland Ecology and Applied Population Ecology. In 2016 she was awarded with the Outstanding Teaching Assistant award for her work as a teaching assistant in Applied population

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*Dedicated to my parents for their support throughout this process and to my grandmother, Muriel Kaplan (Cornell class of 1946), for supporting my education and encouraging my intellectual pursuits.*

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## PREFACE

### **I. Background**

Ecosystem-based management of natural resources has become a dominant paradigm in conservation science and the establishment of marine protected areas is one approach that can be used to implement such conservation strategies (Halpern et al. 2010). The objective of ecosystem-based management strategies is to maintain the long-term sustainability of marine ecosystem services such as fisheries, clean water, aesthetic value, renewable energy, protection from coastal storms, recreational opportunities and tourism by focusing on the integrated process that facilitates ecosystem well-being and human health (Brodziak & Link 2002; Levin et al. 2009). The critical need for effective ecosystem-based management is ubiquitous in the scientific literature (Brodziak & Link 2002; Pikitch et al. 2004; Smith et al. 2007; Levin et al. 2009); however, the complexity and uncertainty surrounding marine ecosystem dynamics and fishery resources has made implementation of these strategies challenging in many situations.

Overfishing is one of the major threats to the integrity of marine ecosystems and marine protected areas (MPAs) are one method that can be effective in protecting species (Halpern 2003; Micheli et al. 2004; Babcock et al. 2010; Edgar et al. 2014). MPAs that restrict fishing to specific zones can be analyzed as human exclusion “experiments”, which in conjunction with recent technological advances for observing ecosystem processes, provide novel opportunities for scientists to understand how management actions affect ecological processes that protect the integrity of habitat and drive the spatiotemporal distributions of fishery resources. Information on the impacts of fishing beyond target species is invaluable to managers looking to assess the ecosystem-wide effects of fishery management actions. By observing the effects of management actions such as closing and opening areas to fishing on the ecology of target and non-target

species, we can begin to implement strategies that incorporate ecological processes thereby reducing uncertainty in resource management. Previous research on MPAs has demonstrated that different life history strategies and ecological functions must be protected in order for protected areas to be effective in an ecosystem context (Palumbi 2004). Life history characteristics such as mobility, body size, habitat requirements and association with benthic habitats can influence species responses to protection in an MPA (Micheli et al. 2004; Garcia & Cochrane 2005; Ashworth & Ormond 2005; Tupper 2007). Determining MPA impacts on specific ecological relationships is therefore paramount to fully evaluating their utility.

Beginning in the 1990s marine protected areas became a more widely used management approach as many fisheries experienced declines. For example, clear management failures leading to the collapse of a number of fisheries in the 1990s, most dramatically the cod (*Gadus morhua*) fishery on Georges Bank, led managers and conservationists to seek alternative management efforts such as the implementation of protected areas. Two chapters from this work evaluate the ecological interactions occurring in Closed Area II of Georges Bank, which was originally put in place primarily to protect groundfish such as cod, though it has been more successful in contributing to higher yields in the Atlantic scallop fishery. The work from this study evaluates the influence of this large protected area on invertebrate ecology. However, it is important to understand the historical underpinnings of the closed areas of Georges Bank and their original intent, as well as how the experience in this region has shaped trends in marine management worldwide.

MPA advocates in the 1990s claimed fishery yields would be improved by MPA establishment. However, by the late 2000s the utility of MPAs was extended to include the primary purpose of protecting biodiversity rather than being implemented with the sole objective



of increasing fishery yields. The number of marine protected areas has grown exponentially in the past 15 years (Lubchenco & Grorud-Colvert 2015). The Convention on Biological Diversity has set a target to protect at least ten percent of coastal and marine areas by 2020, though the current level of protection worldwide is around 3.5%, with 0.59% in no-take marine reserves (Lubchenco & Grorud-Colvert 2015).

In cases where MPAs are established for general conservation, expectations frequently also include increases in fishery yield resulting in an overlap of conservation and fisheries objectives. However, the methods for studying the consequences of conservation and fishery management actions often differ greatly, leading potentially to a mismatch of methods and study objectives. Nonetheless guidelines for a MPA network design that reduce the tradeoff of conservation and fishery goals have been developed (Gaines et al. 2010). Generally biomass of target species increases in MPAs, although there can be a large range of responses (Halpern et al. 2004; Lester et al. 2009). Numerous studies have outlined the variety of ecosystem responses to MPAs including the time it takes to see an effect after implementation (Halpern & Warner 2002; Micheli et al. 2004; Russ et al. 2008; Claudet et al. 2010), the types of species that can and cannot benefit from their implementation (Hilborn et al. 2004; Russ et al. 2004; Hart 2006; White & Kendall 2007; Kaplan 2009), and cascading effects through trophic levels as a result of their implementation (Micheli et al. 2004; Baskett 2006; Baskett et al. 2007).

A study has identified five conditions under which MPAs are most likely to increase abundance of fish: no-take marine reserves; the presence of effective enforcement; in place for a significant period of time; large; and isolated by distance from habitat barriers (Edgar et al. 2014). Empirical data from the Edgar et al. 2014 study indicate that MPAs will increase the abundance of target species inside reserves when these conditions are met. This dissertation

includes MPAs that meet some of these conditions, for example Closed Area II of Georges Bank is a large well-enforced MPA that has been closed to bottom-fishing since 1994. Yield from target fisheries such as the Atlantic sea scallop have increased dramatically since the closed areas have been implemented (Hart & Rago 2006). Additionally, since enforcement has been identified as a key feature of a successful MPA, this dissertation evaluates 21 MPAs from the Greater Caribbean region and assesses the utility of governance strategies for compliance in a region that is varied in terms of the strength of its governing institutions.

Together these studies provide a background for understanding the effects of MPAs as demonstrated in different ecological and managerial contexts. Their utility in these different systems can be evaluated to provide a holistic representation of the conservation value of MPAs from both a local and global perspective. As ecosystems respond to impacts from continually expanding human influence, ensuring that resources are managed sustainably is essential for future generations to meet their needs. MPAs are one management tool that can aide in protecting fishery resources and meeting conservation goals, however fully assessing the implementation and effects of MPAs on ecological processes is necessary to understand both their potential and limitations.

## **II. Study Objectives**

In this dissertation, I provide a contribution to our understanding of MPAs in terms of their governance and their impact on ecological interactions. Understanding resource user behavior and compliance with MPA regulations is essential to evaluating the efficacy of MPAs as a tool for marine management. Evaluating the human dimensions and regulatory efforts leading to successful MPA governance is also necessary to ensure that MPAs are implemented properly and have the greatest chance of success in reaching management objectives. Other studies have indicated that enforcement is one of the key features enabling MPAs to reach their conservation

potential (Edgar et al. 2014). Therefore, evaluating specific enforcement strategies contributes to our understanding of one main aspect of successful MPA governance.

Furthermore, evaluating the impacts of MPAs on ecological relationships is necessary to fully understand their effects in terms of both target species and non-target species. Implementing ecosystem based management requires an analysis of the ecosystem wide effects of processes such as fishing as well as the value protected areas can add to ensuring ecosystem structure and function remain intact. For example, anthropogenic impacts such as the spread of invasive species may be exacerbated by fishing since some invasive species spread using commercial vessels as a vector. Therefore, MPAs may serve as a refuge for many marine populations by keeping habitats intact and reducing degradation by fishing and other anthropogenic influences such as introduced species. Furthermore, MPAs have utility in protecting ecological relationships that can serve as a guide for how organisms interact in environments where human influence is limited or excluded. By comparing these protected areas to areas open to fishing pressure we can gain a fuller understanding of the extent of the consequences of extractive fishing activities. Overall the work presented here provides an understanding of how successful governance of MPAs influences ecosystem function by protecting ecological relationships among target and non-target species. Below, I describe the rationale for each chapter, the study objectives and individual hypotheses investigated. A summary of the key findings are briefly presented following this overview.

*a. Chapter 1: Linking ecological condition to enforcement of marine protected area regulations in the greater Caribbean region*

MPAs are designed to manage human behavior by restricting fishing access in ecologically sensitive areas. Thus, a full understanding of the potential utility of an MPA must be placed in the context of managing human behavior. A primary challenge with implementing MPAs worldwide is ensuring enforcement is adequate and that resource users abide by

regulations. Thus, I evaluated different types of governance strategies designed to promote compliance with MPA regulations in several countries in an attempt to identify effective governance mechanisms for promoting sustainable resource use. The objective of this chapter is to demonstrate the potential of multi-country comparisons in exploring complex social-ecological systems, by examining the relationships between various styles of marine resource governance and the associated indicators of ecological condition inside MPA boundaries within the Greater Caribbean. I explored the influence of both penalties and incentives in promoting compliance with marine resource use regulations in 21 MPAs in the greater Caribbean region. I synthesized existing data on MPA governance (Mascia 1999) and ecological condition (AGRRA, agrra.org) to explore how variation in MPA governance shapes ecological condition within MPA boundaries. This study focuses on correlations between the strategies used to promote compliance with MPA regulations and ecological indicators such as the biomass and density of commercially significant fish species, fish in various functional groups, as well as percentages of live hard coral cover within the studied MPAs. Fish metrics of commercially-valued species, in particular high trophic level species such as snappers and groupers, are widely used to evaluate the effects of fishing on coral reefs (Chiappone et al. 2000). The life history characteristics of these commercial species such as large body size and slow and late maturity make them highly vulnerable to the fishing pressure, thus these species are necessary to consider in conservation strategies (Kaplan et al. 2014). For this study I hypothesized that enforcement strategies which use a higher number of penalties and incentives to promote compliance with MPA regulations will be positively correlated with more sustainable resource use resulting in greater fish biomass and density of commercial species.

b. *Chapter 2: The distribution of the invasive tunicate (Didemnum vexillum) in Atlantic sea scallop (Placopecten magellanicus) habitat on fishing grounds and a large protected area of Georges Bank*

While the success of MPAs in promoting increases in fish biomass in some fisheries has been well-documented, less is known about how MPAs might serve to protect against impacts from invasive species. An invasive colonial tunicate (*Didemnum vexillum*) has been located both inside and outside of the MPAs on Georges Bank since its initial discovery in 1998. For this chapter I determined if the invasive *D. vexillum* competes for habitat with the region's most valuable fishery, the Atlantic sea scallop. The habitat camera mapping system (HabCam), a vessel-towed underwater camera system, was utilized to explore the spatial distribution of sea scallops and *D. vexillum* in protected and unprotected areas of Georges Bank. I assessed if this invasive species negatively correlates to the distribution of sea scallops and evaluated the potential role MPAs play in limiting the invasive species' expansion. The closed areas of Georges Bank provide an important opportunity to determine how bottom fishing affects benthic community structures since large sections have been closed to bottom fishing since 1994. Activities such as scallop dredging and bottom trawling may have the potential to facilitate the spread of the invasive *D. vexillum* due to increased colony fragmentation (Morris & Carman 2012), or the disturbance from bottom-fishing may create more preferable habitat for *D. vexillum*, though further studies are necessary to evaluate specific mechanisms of its spread. I hypothesized that areas open to fishing will have greater concentrations of the invasive *D. vexillum* and that there will be a negative relationship between *D. vexillum* and sea scallops due to the tunicate's ability to prevent settlement of scallop spat and perhaps also increase mortality of adults (Morris et al. 2009). This work furthers our understanding of invasive species effects

and how species interactions may be influenced by the use of protected areas. Possible management actions designed to mollify the negative impacts of the invasive *D. vexillum* on essential fish habitat are also discussed in this chapter.

*c. Chapter 3: Invasive tunicate restructures invertebrate community in fishing grounds and a large protected area on Georges Bank*

This study assesses the impacts of the invasive tunicate *Didemnum vexillum* on invertebrate species in the benthic community and how these interactions are affected by bottom-fishing as compared to those occurring in the protected area. Fishing impacts myriad species and processes beyond the fishery, which is evident from numerous studies on the problem of bycatch and habitat destruction. Only through a full understanding of the consequences of alternative management options beyond target species can we begin to fully comprehend the impact that implementing ecosystem-based strategies have for fishery management. The HabCam system can be used, among other things, to address questions related to the extent of damage bottom-fishing incurs in benthic marine habitats. Several studies indicate that dredging disturbances reduce the diversity and abundance of benthic communities in the region (Collie et al. 1997; Auster et al. 1996). Further studies show that bottom fishing gear damages epifaunal taxa and thus reduces habitat complexity (Jennings and Kaiser 1998; Fogarty and Muraski 1998). Additionally, invasive species may be degrading valuable fishery habitat in this region, which potentially is exacerbated by fishing effects. Evaluating the ecosystem level effects of these processes will provide valuable information to managers to fully assess the impact of management actions beyond the target species.

For this chapter, I hypothesized that *D.vexillum* would demonstrate a negative

relationship with most other invertebrate benthic species due to its acidic colony surface and allelopathic compounds present in its tunics. I used the habitat camera mapping system (HabCam) to explore the spatial distribution of benthic marine invertebrates and *D. vexillum* in areas protected and unprotected from bottom-fishing on Georges Bank to test if benthic invertebrates are negatively correlated with this invasive species. I also assessed how the invertebrate community changes in the presence of *D. vexillum* using multivariate data analysis. Additionally, I evaluated if the abundances of these invertebrates is greater in areas open or closed to bottom-fishing. I hypothesized that habitat degradation may be occurring due to the combined effects of the invasive tunicate and bottom-fishing. Multivariate data analysis was used to identify fishing effects and invasive species effects separately. The interactions among benthic organisms are structured by both the invasive species spreading across the habitat and the effects of fishing. This work can further our understanding of ecological interactions occurring in the benthic community of MPAs and the role MPAs play in structuring these interactions.

### **III. Description of key findings**

#### *a. Chapter 1: Linking ecological condition to enforcement of marine protected area regulations in the greater Caribbean region*

This study included a review of literature on compliance with MPA regulations and an exploratory data analysis to evaluate links between strategies used to promote compliance with MPA regulations and indicators of ecological condition for 21 MPAs in 13 different countries and territories of the Greater Caribbean region. The results from this study found an increase in the number of incentives and penalties was positively correlated with higher commercial fish biomass in Caribbean MPAs. Although, penalties are generally employed to enforce regulations, this study highlights that incentives may also play an important role in governing successful MPAs. Additionally, an interaction between penalties and incentives showed that these methods

together may be more effective than using penalties alone. The sustainable and efficient management of resources is conditioned on the imposed regulations being controlled and enforced. However, in developing countries resources for enforcement may be lacking. Therefore, incentives may provide added returns on efficacy compared to the investment required to provide them. Additionally, other studies have supported that interactions among incentives can lead to governance systems that are more resilient in protecting marine areas from anthropogenic and natural perturbation (Jones 2014).

b. *Chapter 2: The distribution of the invasive tunicate (Didemnum vexillum) in Atlantic sea scallop (Placopecten magellanicus) habitat on fishing grounds and closed areas of Georges Bank*

This study evaluated the invasion of *Didemnum vexillum* on Georges Bank and demonstrated a negative correlation with the Atlantic sea scallop. The Atlantic scallop is currently the highest valued fishery in the region with profits reaching about \$500 million annually. Both scallop and *D.vexillum* prefer gravel habitat that also serves as nursery habitat for juvenile fishes. The species distributions were analyzed visually using data collected from the vessel-towed underwater imaging system (HabCam). The distribution of the invasive tunicate was significantly greater in the area open to bottom-fishing, which is actively dredged. Additionally, *D.vexillum* can reproduce asexually and colony fragmentation from dredging may also be a possible mechanism for its spread, though more data is necessary to investigate this hypothesis. Overall, the results from this study demonstrate the spread of an invasive tunicate that may affect habitat of a valuable invertebrate fishery on Georges Bank.

c. *Chapter 3: Invasive tunicate restructures invertebrate community on fishing grounds and closed areas of Georges Bank*

For this chapter, I assessed the impact of the invasive tunicate (*D.vexillum*) on the invertebrate



community of Georges Bank. I used data from the habitat camera mapping system to determine densities of invertebrates and I modeled individual interactions of invertebrates with *D.vexillum*. When present in the invertebrate community, *D.vexillum* is a major driver of variation among sites analyzed. Some species reassociate based on a positive or negative response to its presence. It appears to restructure the invertebrate community when present forming a distinct grouping around it in both open and closed areas. Additionally, the community it forms generally are with species that are more abundant in the area open to bottom-fishing, though associations for most species with *D.vexillum* are consistent even in the closed area. I observed that associations among species were more diffuse and not as closely clustered in the area open to fishing as compared to the closed area, indicating that bottom-fishing may alter ecological interactions occurring among species. *Didemnum vexillum* may colonize space opened up by bottom-fishing, resulting in a synergistic interaction leading to habitat degradation, though more data may be necessary to assess this hypothesis. In summary, I provide evidence of *D.vexillum* restructuring the invertebrate community on Georges Bank and demonstrate the consequences that a protected area can have on these interactions as compared to areas open to fishing.

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## CHAPTER 1

# LINKING ECOLOGICAL CONDITION TO ENFORCEMENT OF MARINE PROTECTED AREA REGULATIONS IN THE GREATER CARIBBEAN REGION

### **Abstract**

Marine protected areas (MPAs) are increasingly employed worldwide to conserve marine resources. However, information on the role of governance mechanisms, in particular those associated with compliance, in shaping ecological condition inside MPAs at the regional scale remains deficient. An exploratory data analysis was conducted to evaluate links between strategies used to promote compliance with MPA regulations (e.g. incentives and penalties) and indicators of ecological condition, including biomass and density of commercial fish species, fish functional groups and coral cover in 21 MPAs across 13 different countries and territories in the greater Caribbean region. The strategies used to promote compliance with MPA regulations were correlated with indicators of ecological condition. For example, MPAs in which a larger number of incentives and penalties are present in the governance system are associated with higher commercial fish biomass and density as compared to those with fewer penalties and incentives available to promote compliance. Although most MPAs in the greater Caribbean use penalties to enforce compliance, our results suggest incentives may also be an important governance strategy for ensuring efficacy of protected areas in conserving key species. Alternatively, the presence of a high number of penalties and incentives in governance systems may also be indicative of greater state capacity and political will in these MPAs resulting in better managed MPAs. Further research is necessary to evaluate results of the exploratory data analysis presented in this study with a more in depth analysis of the de facto use of the regulations evaluated and their

efficacy. Multi-country comparisons of MPA governance and ecological indicators can help policy and decision makers maintain MPAs that most effectively achieve MPA conservation objectives. (Originally published as Kaplan et al. 2015).

## **1. Introduction**

Marine protected areas (MPAs) are increasingly employed worldwide as an ecosystem-based management strategy used to prevent the degradation of sensitive marine ecosystems and to manage and conserve ecosystem services such as fisheries, coastal protection, habitat restoration, biodiversity conservation and tourism (Palumbi 2004; Edgar et al. 2007; Halpern et al. 2008, 2010). MPAs are key strategies for sustaining ecosystem services particularly in tropical developing countries where regulation of catch and fishing effort are challenging in the prevalent multi-species, multi-gear, small-scale fisheries (Gutiérrez et al. 2011). The management of MPAs has relied on a diverse set of governance strategies, which have included penalties, incentives and appeals to user values, attitudes, and beliefs (Kuperan & Sutinen 1998; McCay & Jones 2011; Jones et al. 2013; Jones 2014a). While much funding and effort has been put into the development of MPAs (Edgar et al. 2007, 2014; Guarderas et al. 2008; Jones 2014b) those governance strategies that lead to positive social and environmental outcomes remain poorly understood (Fox et al. 2012b, 2014). Wide variation has been observed in the effects of MPAs on ecological (Halpern 2003; Micheli et al. 2004; Mumby 2006; Lester et al. 2009; Babcock et al. 2010) and social factors (Mascia 2003; Klein et al. 2008; Mascia & Claus 2009; Mascia et al. 2010), yet explanations of the drivers of this variation remain tenuous. MPAs that fail to meet conservation goals are often labeled “paper parks”, existing only in name (Mora et al. 2006; McClanahan et al. 2006; Christie & White 2007). Large-scale multi-country

comparisons of governance features and scientific studies measuring the impacts of MPAs are necessary to understand the aspects of MPA management that are linked to positive outcomes such as maintaining ecosystem structure, function, and delivery of ecosystem services (Halpern et al. 2008; Fox et al. 2012a, 2014).

In this paper, we examine the potential of multi-country comparisons in exploring complex social-ecological systems, by examining the relationships between marine resource governance and indicators of ecological condition inside MPA boundaries within the Greater Caribbean. We focus on governance strategies used to promote compliance with marine resource use regulations that govern who may use marine resources, as well as how, when and where they may use them. The likelihood of compliance with marine resource regulations is shaped by multiple factors including individual-level factors and perceptions, regulatory enforcement, as well as incentives and regulatory alternatives.

### *1.1 Individual-level factors and perceptions*

At the individual level, fisher perceptions of the regulatory process and its outcomes are significant drivers of compliance behavior in marine contexts (Table 1). Moral obligation, social influence, shared norms and perceived legitimacy of authorities charged with implementation of regulations are important factors influencing fisher adherence to regulations (Ostrom 1990; Kuperan & Sutinen 1998; Hatcher et al. 2000). Regulations must be perceived by fishers as biologically meaningful and effective in conserving fish stocks (Raakjær Nielsen & Mathiesen 2003). Prevailing distrust among fishers for the work of fisheries scientists and the belief that regulations lack biological efficacy in conserving stocks can negatively affect fishers' decision to comply with regulations (Raakjær Nielsen & Mathiesen 2003). Therefore, fisher perceptions of the legitimacy of the regulations matter greatly (Kuperan & Sutinen 1998; Raakjær Nielsen



2003; Viteri & Chávez 2007) . However, compliance is not only influenced by perceived legitimacy of regulations, but also the perceived legitimacy of the process for enforcing regulations (Raakjær Nielsen 2003) . Compliance has been shown to increase when monitoring of behavior and penalties for noncompliance is accountable, legitimate, and equitable (Raakjær Nielsen 2003). Finally, fisher perceptions of how the process affects themselves and their livelihoods relates to compliance behavior (McClanahan et al. 2005). The distribution of benefits and costs among MPA stakeholders as a result of regulations must be perceived as fair, as must fisher perceptions of how respectfully they are treated by enforcement authorities (Alder et al. 1994; Kuperan & Sutinen 1998; Hønneland 2000).

### *1.2 Regulatory enforcement*

Governance attributes designed to promote compliance have been shown to encourage sustainable resource use (Table 1). Monitoring and enforcement of MPA regulations organized via graduated sanctions in which rule violators are punished based on the severity and context of offense and the characteristics of the violator are considered a successful tool (Ostrom 2008). A lack of enforcement leading to regulatory noncompliance is often cited as a main cause of failure for many MPA management strategies (Crawford et al. 2004; McClanahan et al. 2006; Edgar et al. 2014), while increased enforcement of regulations and subsequent compliance has been correlated to higher fish biomass and richness on a global scale—two indicators of successful conservation (Pollnac et al. 2010; Edgar et al. 2014).

Classic enforcement models indicate that individuals are deterred from violating regulations when the probability of detection is high and the penalty is severe, outweighing the potential for illegal gains (Kuperan & Sutinen 1998; Raakjær Nielsen 2003). However, for illegal fishing in many countries the probability of detection and conviction is usually low and

sanctions are often lenient and uncertain; thus, the penalties frequently do not offset financial gains, leading to violations (Kuperan & Sutinen 1998). For example, previous failures in marine management due to high levels of non-compliance behavior in ground fish fisheries on the US East Coast can partially be explained by the relatively low economic sanctions compared to large economic gains obtained from illegal fishing as well as distrust among stakeholders groups (Kaplan & McCay 2004). Therefore, in the context of marine resources and illegal fishing, while surveillance and severity of sanctions are important, they may not necessarily be the decisive factors influencing compliance (Hønneland 2000).

Regulatory enforcement is costly and in developing countries in particular resources available for conservation purposes are often limited (Balmford et al. 2002). High transaction costs required to monitor and enforce MPAs as well as the high levels of management costs may necessitate a conjunction of methods used to promote compliance (Naidoo et al. 2006). Incentives may provide added levels of efficacy and may be more cost-effective compared to the monitoring and enforcement of penalties (Hutton & Leader-Williams 2003). In addition to the costs of a penalties-based approach for MPA management and enforcement, penalties come at a cost for the fishers as well (Raakjær Nielsen 2003; Gjertsen & Niesten 2010). In a penalty scenario, fishers are forced to weigh the costs of sanctions with the benefits of breaking the rules; incentives create scenarios that diminish the opportunity costs of abiding by the rules since by abiding by the regulations they experience gains (Hutton & Leader-Williams 2003; Hilborn et al. 2005; Gjertsen & Niesten 2010). Therefore, consideration of incentives as an addition to penalties for encouraging desired fisher behavior might be worthwhile.

### *1.3 Incentives*

Incentives that address the individual-level factors and perceptions, as discussed earlier,

have been shown to aid in encouraging compliance behavior (Table 1). Incentives are defined in this study as regulatory measures designed to encourage resource users to act in accordance with strategic policy outcomes intended for MPA objectives to be achieved (Jones 2014a). Similar to classifications of incentives from previous studies (Jones 2014a), incentives can be categorized as economic (i.e. market-based solutions and property rights used to achieve MPA objectives), participative (i.e. participation of local users in management decisions), interpretative (i.e. promoting awareness of conservation features, regulations and restrictions, and benefits of the MPA) or knowledge based (i.e. respecting and promoting different sources of knowledge from local-traditional to expert-scientific as well as methods for addressing uncertainty and knowledge deficits). Participatory incentives such as, empowering local users to control resource access and enforce regulations in small-scale fisheries has been shown to promote sustainable resource use in some cases (Basurto 2008; Basurto & Coleman 2010). Collective choice decision-making arrangements are hypothesized to enhance the sustainability of marine resource governance systems by fostering a shared sense of ownership encouraging responsible fishing (Basurto 2008; Ostrom 2009; Basurto & Coleman 2010; Gutiérrez et al. 2011), greater sensitivity to socioeconomic and ecological constraints (Gutiérrez et al. 2011), increased compliance with regulations through peer pressure (Raakjær Nielsen 2003), as well as greater transparency and accountability of monitoring and enforcement (Basurto 2005a).

Economic incentives such as rights-based management schemes for fisheries in which restrictions are placed on access to the fishery through methods such as catch shares have been successful in many cases (Costello et al. 2008). Rights-based management schemes create incentives for resource users to conserve fish by providing fishers economic property rights to the fishery, which ensures fishers bear the costs of overexploitation (Hilborn et al. 2005; Grafton

et al. 2006). Additionally, development of alternative livelihoods to reduce destructive fishing practices has been effective for promoting pro-conservation behavior in some MPAs (Nur et al. 2001). Other economic incentives may include providing compensation to resource users who bear costs due to MPA restrictions such as buybacks of fishing vessels, licenses, access, gear, use or other rights (Macintosh et al. 2010; Squires 2010; Jones 2014a). Interpretative incentives include public communication, education and awareness on the significance and susceptibility of marine ecosystems to anthropogenic and natural threats and the benefits of the MPA (Petrosillo et al. 2007; Leisher et al. 2012; Jones et al. 2013). These incentives may also include promoting awareness of MPA regulations and restrictions to promote compliance with regulations (McCAY & Jones 2011; Leisher et al. 2012; Jones et al. 2013). Additionally knowledge-based incentives include incorporating different types of knowledge from local and indigenous to expert to form MPA management strategies (Drew 2005; Aswani & Lauer 2006; Gerhardinger et al. 2009; Jones 2014a). Knowledge-based incentives may also include strategies for managing uncertainty, data deficiency and conflicting objectives when making MPA management decisions (Wood & Dragicevic 2006; Salomon et al. 2011; Jones 2014a; Kaplan et al. 2014). Studies have focused primarily on penalties used to enforce protected area regulations (Viteri & Chávez 2007; Edgar et al. 2014); given the potential for incentives to promote compliance with regulations we explore links between incentives and penalties on ecological indicators in MPAs.

Table 1.1 Factors influencing resource user compliance with MPA regulations

Individual level factors & perceptions	Source
Regulations perceived as biologically meaningful	(Raakjær Nielsen & Mathiesen 2003)

Regulations perceived as legitimate	(Raakjær Nielsen 2003; Viteri & Chávez 2007)
Authorities perceived as legitimate	(Raakjær Nielsen 2003; Viteri & Chávez 2007; Gutiérrez et al. 2011)
Sense of moral obligation	(Kuperan & Sutinen 1998; Hønneland 2000; Raakjær Nielsen 2003)
Treated respectfully by authorities	(Kuperan & Sutinen 1998; Raakjær Nielsen 2003)
Perceived fairness in cost/benefit distribution	(Alder et al. 1994; Kuperan & Sutinen 1998; Raakjær Nielsen 2003)
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Regulatory enforcement factors	Source
Enforcement strategy exists	(Crawford et al. 2004; McClanahan et al. 2006)
High probability of violators being detected	(Kuperan & Sutinen 1998; Raakjær Nielsen 2003)
High penalty for violation	(Kuperan & Sutinen 1998; Raakjær Nielsen & Mathiesen 2003; Kaplan & McCay 2004)
Graduated sanctions for violations	(Ostrom 2008, 2009)
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Participatory incentives	Source
Opportunity for self-control and self-enforcement	(Basurto 2005b, 2008; Ostrom 2009; Basurto & Coleman 2010; Gutiérrez et al. 2011)
Co-management of MPAs with fishers	(Basurto 2005b, 2008; Ostrom 2009; Basurto & Coleman 2010; Gutiérrez et al. 2011)
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Economic incentives	Source
Provision of alternative livelihoods	(Nur et al. 2001)

Rights based management schemes	(Hilborn et al. 2005; Costello et al. 2008)
Buyback for fishing gear, licenses or rights	(Macintosh et al. 2010; Squires 2010; Jones 2014a)
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Interpretative incentives	Source
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Public communication, education and awareness of MPA objectives and benefits	(Petrosillo et al. 2007; Leisher et al. 2012; Jones et al. 2013)
Promoting awareness of MPA regulations and restrictions	(McCAY & Jones 2011; Leisher et al. 2012; Jones et al. 2013)
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Knowledge-based incentives	Source
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Incorporating different types of knowledge	(Drew 2005; Aswani & Lauer 2006; Gerhardinger et al. 2009; Jones 2014a)(McCAY & Jones 2011; Leisher et al. 2012; Jones et al. 2013)
Managing uncertainty, data deficiency and conflicting objectives	(Wood & Dragicevic 2006; Salomon et al. 2011; Jones 2014a; Kaplan et al. 2014)
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#### *1.4 Study aims*

We explored the link between both penalties and incentives intended to promote compliance with marine resource use regulations and indicators of ecological condition in 21 MPAs in the greater Caribbean region. We synthesized existing data on MPA governance (Mascia 2000), Mascia unpublished data, and ecological condition (AGRRA, agrra.org) to explore how variation in MPA governance shapes ecological condition within MPA boundaries. Our study focused on correlations between the strategies used to promote compliance with MPA regulations and ecological indicators such as the biomass and density of commercially significant fish species and fish in various functional groups as well as percentages of live hard coral cover within the studied MPAs. Fish metrics of commercially-valued species, in particular carnivores such as snappers and groupers, are widely used to evaluate the effects of fishing on coral reefs (Chiappone et al. 2000). The life history characteristics of these commercial species such as large body size and slow and late maturity make them highly vulnerable to the fishing pressure, thus these species are necessary to consider in conservation strategies (Kaplan et al. 2014). We hypothesized that enforcement strategies which use a higher number of penalties and incentives to promote compliance with MPA regulations would be positively correlated with more sustainable resource use resulting in greater fish biomass and density of commercial species. This study uses quantitative techniques to explore links between governance and ecological data though further analysis using qualitative analysis may be necessary to evaluate the results indicated.

## **2. Methods**

### *2.1 Study area*

The number of MPAs in the greater Caribbean region has increased rapidly since the 1980s and currently totals over 800 (Guarderas et al. 2008; “WDPA Consortium World Database on Protected Areas.” 2012). Although the ecological and social conditions of MPAs in the Caribbean vary substantially (Guarderas et al. 2008), the general consensus is that fish stocks are depleted and severely overfished in some areas (Jackson et al. 2001, 2014; Cramer et al. 2012). In addition to problems of overfishing, global climate change and the spread of marine diseases in Caribbean MPAs have furthered coral reef decline (Aronson & Precht 2006; Carpenter et al. 2008; Jackson et al. 2014). The loss of coral cover in the region has been significant (Jackson et al. 2001, 2014; Gardner et al. 2003) and studies have highlighted the need for ecosystem-based management strategies focusing on maintaining the resilience of marine ecosystems to a variety of perturbations (Bellwood et al. 2004). Despite these challenges, MPAs remain a key strategy in protecting coral reef biodiversity in the Caribbean. Twenty-one MPAs in 13 different countries and territories in the greater Caribbean region were used for analysis in this study (Figure 1.1), with the corresponding number of ecological sites analyzed inside each MPA with the area and date of establishment (Table A1). The 21 MPAs were selected as sites that overlapped from the Atlantic Reef Rapid Gulf Assessment Program ([agrra.org](http://agrra.org)) and the marine resource governance survey collected by Mascia 2000 (Mascia 2000), Mascia unpublished data.



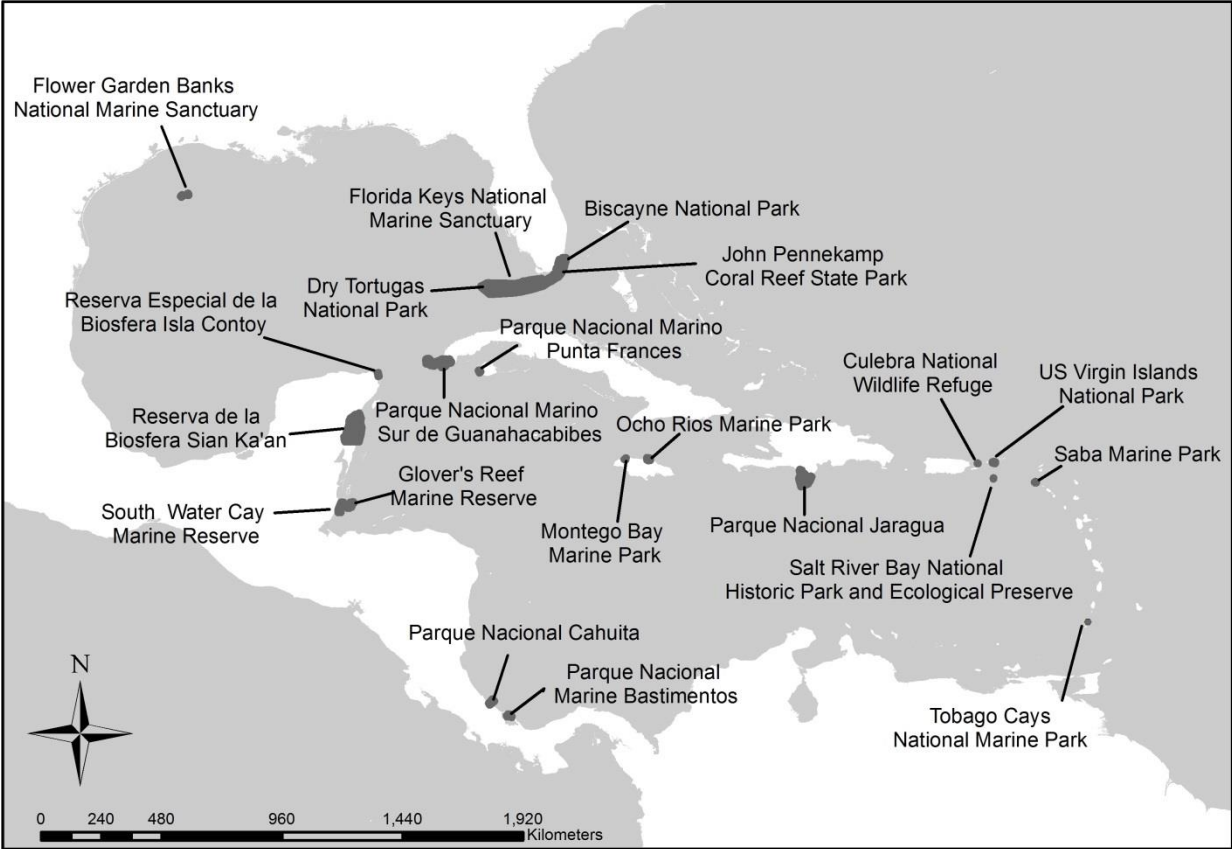


Figure 1.1. Map of 21 Caribbean MPAs analyzed in this study.

## *2.2 Enforcement of regulations data*

We draw on data collected by Mascia 2000, Mascia unpublished data, to characterize marine resource governance in Caribbean MPAs. Mascia 2000 conducted an international mail survey of MPA managers in the greater Caribbean region in 1999 posing 16 constrained-choice questions focusing on the marine resource governance system in a single MPA based on the methodology described in Mascia 1999. The individual directly responsible for site management in the MPA was chosen as site respondent. Two questions focused on the system of penalties and incentives used to promote compliance with MPA regulations. The respondent was asked if the following penalties were present based on the legal framework governing the MPA: verbal or written warnings, fines, loss of access to natural resource, confiscation of equipment, incarceration, or other. The respondent was also asked if the following incentives were present based on the legal framework governing the MPA: environmental education, skills training, exchange of equipment, purchase of equipment, employment, or other. These incentives can be categorized based on incentive type. Interpretative incentives analyzed include environmental education and skills training. Participatory incentives include employment, while purchase and exchange of equipment are economic incentives. One question identified the marine resource uses permitted in the MPA and the extent to which these uses were zoned based on the legal framework governing the MPA. MPA managers were asked if the harvest of marine life is permitted in all regions of the MPA, restricted in regions of the MPA, or prohibited in the MPA. The survey questions regarding the marine resource uses permitted in the MPA were used to identify impacts of the different commercial use regulations on indicators of ecological condition (Mascia 1999), [www.agrra.org](http://www.agrra.org).

### *2.3 Ecological data from the Atlantic Gulf Rapid Reef Assessment*

We synthesized data from the Atlantic Gulf Rapid Reef Assessment (AGRRA) database ([www.agrra.org](http://www.agrra.org)) to provide a ‘snapshot’ of ecological condition in MPAs of the greater Caribbean region. The AGRRA data were originally collected between 1997-2004 to complete a regional assessment of the health of coral reefs in the Western Atlantic and Gulf of Mexico using a standardized sampling protocol (Table A1). AGRRA sites are surveyed in a probabilistic fashion to yield information representative of large areas, such as shelves, islands, countries or ecoregions, i.e., at the scales over which many reef structuring processes and impacts occur ([www.agrra.org](http://www.agrra.org)). Benthic cover was recorded at 10 cm intervals on each of six 10 m long transect lines, which were conducted at transect lengths of 10 m by 1 m<sup>2</sup> during which the size and condition of all corals greater than or equal to 4 cm were recorded for AGRRA surveys. Benthic cover was recorded via point intercept counts in which substratum was recorded below each 10 cm mark along the transect line. The percent coral cover was calculated as percentage of the total cover of substratum. Substratum was recorded as live coral cover, dead coral, pavement, rubble, sand or other. Furthermore fish biomass and density estimates were also obtained from the AGRRA dataset, which includes fish at the species and family level as well as biomass and density estimates of commercially significant species identified through FishBase ([agrra.org](http://agrra.org); [fishbase.org](http://fishbase.org)). Biomass is estimated by adding the weights of fish by using body-length and the length-weight conversion  $W=aL^b$ , where (W) is the weight in grams, (L) is the body length in cm and (a) and (b) are constants obtained from FishBase. For fish surveys, roving divers determined counts and sizes for all fishes in the water column within 30 m by 2 m wide belt transects. The data used were site-level averages from a series of transects (>4) conducted at each site ([www.agrra.org](http://www.agrra.org); Vallès & Oxenford 2014). Temporal considerations between the time

of governance data collection and ecological data were researched to determine consistency of management regulations during the study time period (Appendix A, Table A1)

#### *2.4 Data analyses*

Survey data related to compliance and marine resource use was connected to ecological indicators for all sites within each MPA for all analyses (Table A1). The number of penalties and incentives present in each MPA was counted and individual penalty types (verbal or written warnings, fines, loss of access to resource, confiscation of equipment, incarceration or other) and incentive types (environmental education, skills training, exchange of equipment, purchase of equipment, employment or other) were correlated to ecological data. Ecological indicators analyzed include site-level averages of percent live hard coral cover, total fish biomass, commercially significant fish species, and several fish functional groups including: herbivore biomass, invertivore biomass, piscivore biomass and parrotfish biomass. Parrotfish were the only group analyzed on the family level because of their well-documented role in maintaining resilience in coral reef ecosystems (Bellwood et al. 2004; Mumby et al. 2013) and they can be used as an indicator of fishing pressure (Vallès & Oxenford 2014). Data from 132 sites within the 21 MPAs were used for all analyses, except for the analysis of incentives as data were lacking from one MPA (Ocho Rios Marine Reserve, Jamaica), thus 20 MPAs were used to analyze the impact of incentives. All statistical analyses were conducted on the R statistical platform v. 2.15.3 (*R Development Core* 2014). In all analyses, stepwise multi-linear regression was used to correlate incentive types and penalties types to ecological variables and the most parsimonious model of all candidate models was selected using Akaike's Information Criterion (Burnham & Anderson 2002) by use of the step AIC function as part of the MASS package [60,61]. We also analyzed spatial auto-correlation of the commercial fish biomass data using

geostatistical methods including the variogram function in the gstat package for R (Pebesma 2004).

### **3. Results**

#### *3.1 Regulations on commercial use*

Commercial species biomass was greater in MPAs in which the harvest of marine life for commercial purposes is illegal (Figure 1.2, ANOVA  $F_{2,107}=4.28$ ,  $p=0.04$ ). There was no statistically significant relationship related to commercial use in the MPA for total fish biomass (ANOVA  $F_{2,107}=0.20$ ,  $p=0.66$ ), herbivore biomass (ANOVA  $F_{2,107}=0.10$ ,  $p=0.74$ ), piscivore fish biomass (ANOVA  $F_{2,107}=0.72$ ,  $p=0.40$ ), invertivore fish biomass (ANOVA  $F_{2,107}=0.09$ ,  $p=0.76$ ), and coral cover (ANOVA  $F_{2,107}=0.87$ ,  $p=0.35$ ).

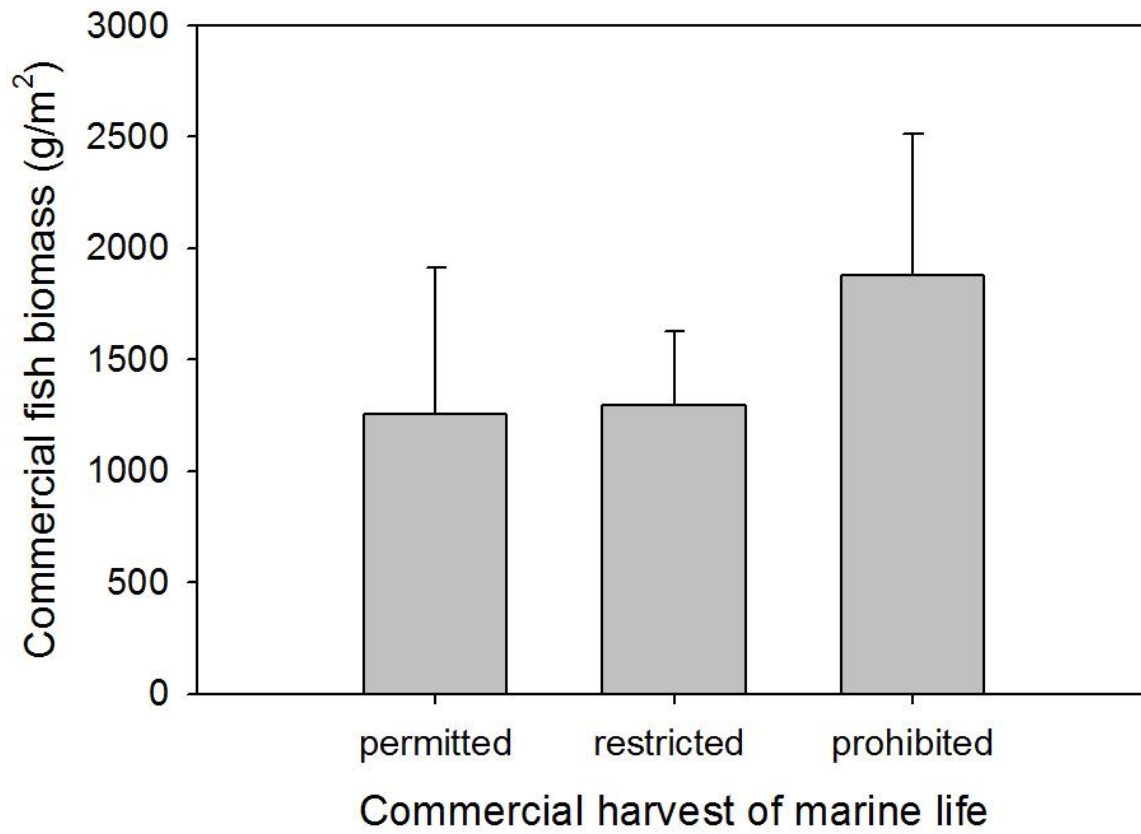


Figure 1.2. Commercial fish biomass (g/m<sup>2</sup>) in MPAs with permitted, restricted and prohibited commercial harvest regulations. ANOVA  $F_{2,107}=4.28$ ,  $p<0.05$ . Error bars= 95% CI.

### *3.2 Penalties and incentives*

A statistically significant correlation was found in MPAs with an increasing number of incentives used to promote compliance with regulations and commercial fish biomass (Figure 1.3,  $F_{3,109}=2.76$ ,  $p<0.05$ ) and a similar relationship was observed between the number of incentives and commercial fish density (Figure 1.4,  $F_{3,109}=5.32$ ,  $p<0.01$ ). Additionally, a similar trend was observed with increasing numbers of penalties and commercial fish biomass, however the relationship was marginally significant (Figure 1.5, ANOVA  $F_{4,111}=2.279$ ,  $p=0.06$ ). The same trend was observed in commercial fish density, which was also marginally significant (Figure 1.6 ANOVA  $F_{4,111}=2.101$ ,  $p=0.09$ ). MPAs that utilized at least four incentives had greater commercial fish biomass and MPAs with five incentives hosted greater commercial fish density and biomass (Figures 1.3 and 1.4). Our sample included no MPAs with three incentives total. The discrepancy between commercial fish biomass and density for four incentives indicates that there are larger fish in this category since biomass is high, while density remains low (Figures 1.3 and 1.4). Also, an interaction effect between incentives and penalties on commercial fish biomass was observed (ANOVA,  $F_{4,118}=4.305$ ,  $p<0.01$ , Figure 1.7). We did not observe a significant relationship between total fish biomass and incentives (ANOVA,  $F_{3,109}=1.713$ ,  $p=0.169$ ) or penalties ( $F_{4,111}=1.649$ ,  $p=0.167$ ). Specific types of penalties did not individually correlate to any fish biomass or density indicators. Specific types of incentives were found to have differential impacts on multiple ecological indicators (Table 1.2).

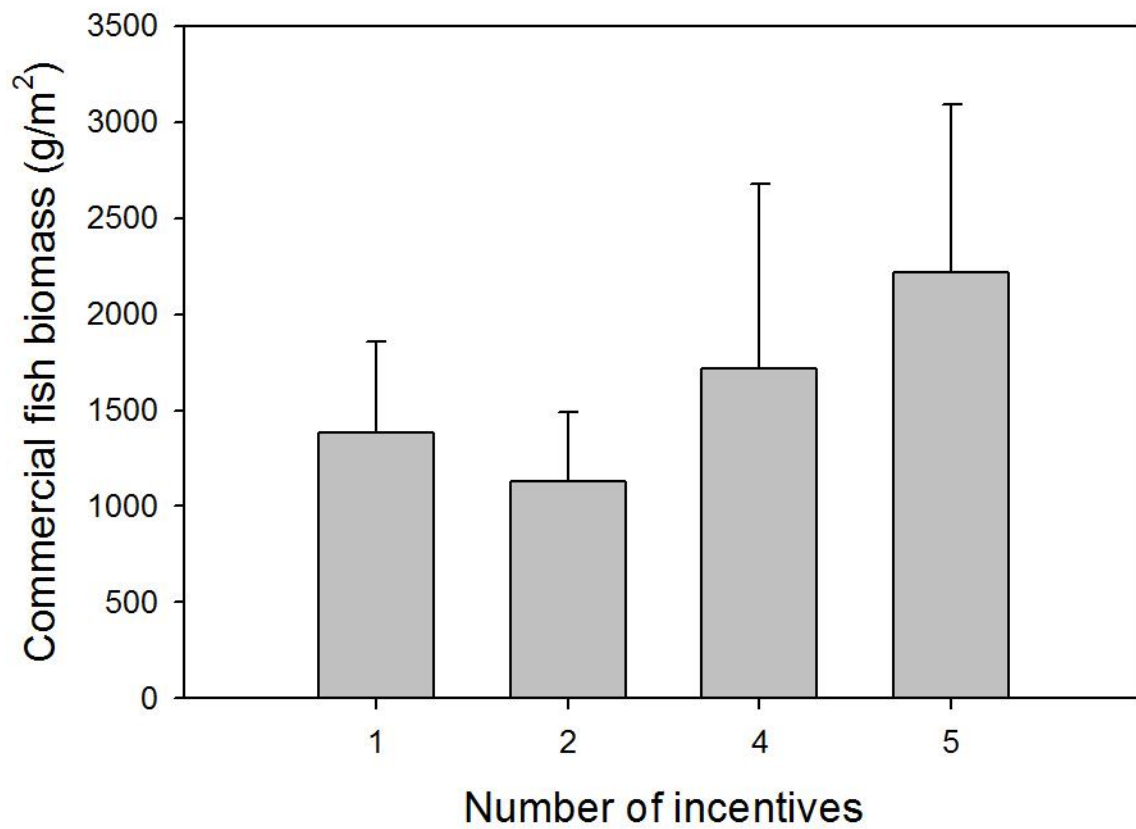


Figure 1.3. Commercial fish biomass (g/m<sup>2</sup>) in MPAs with varying numbers of incentives used to enforce MPA regulations. ANOVA  $F_{3,109}=2.764$ ,  $p<0.05$ . Error bars= 95% CI. No MPAs with exactly three incentives were found in this study.



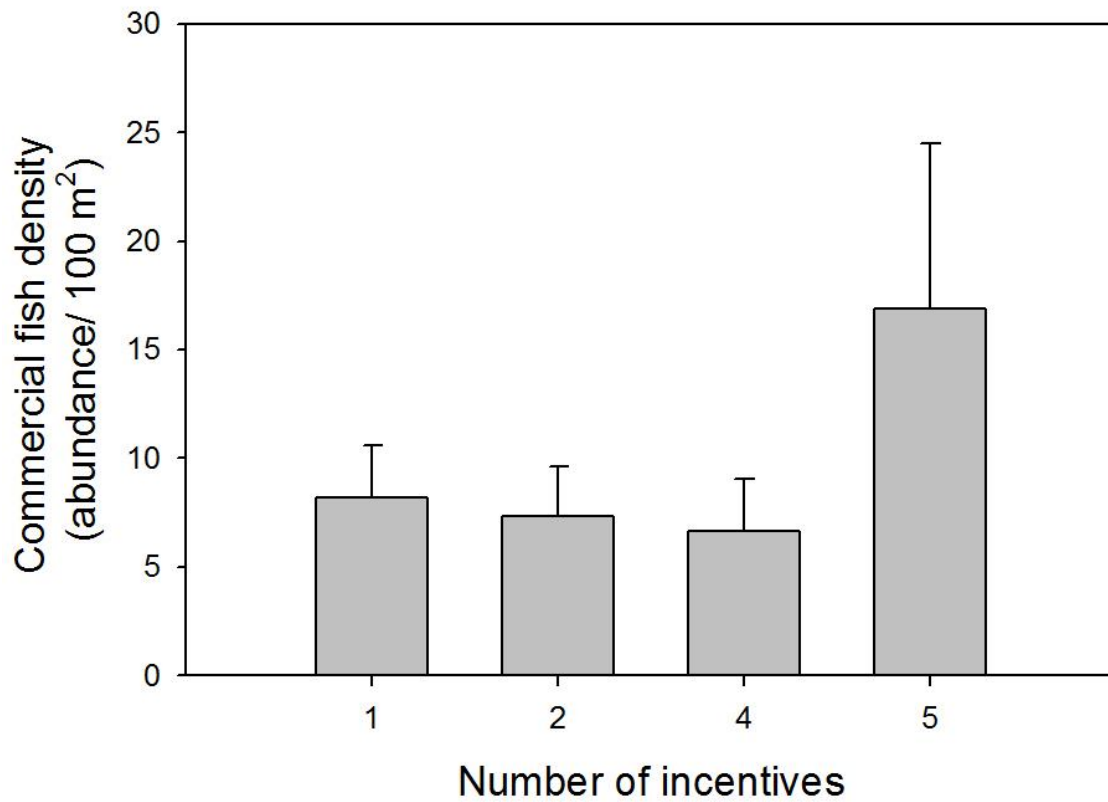


Figure 1.4. Commercial fish density (abundance/ 100 m<sup>2</sup>) in MPAs with varying numbers of incentives used to enforce MPA regulations. ANOVA,  $F_{3,109}=5.320$ ,  $p<0.01$ . Error bars= 95% CI.

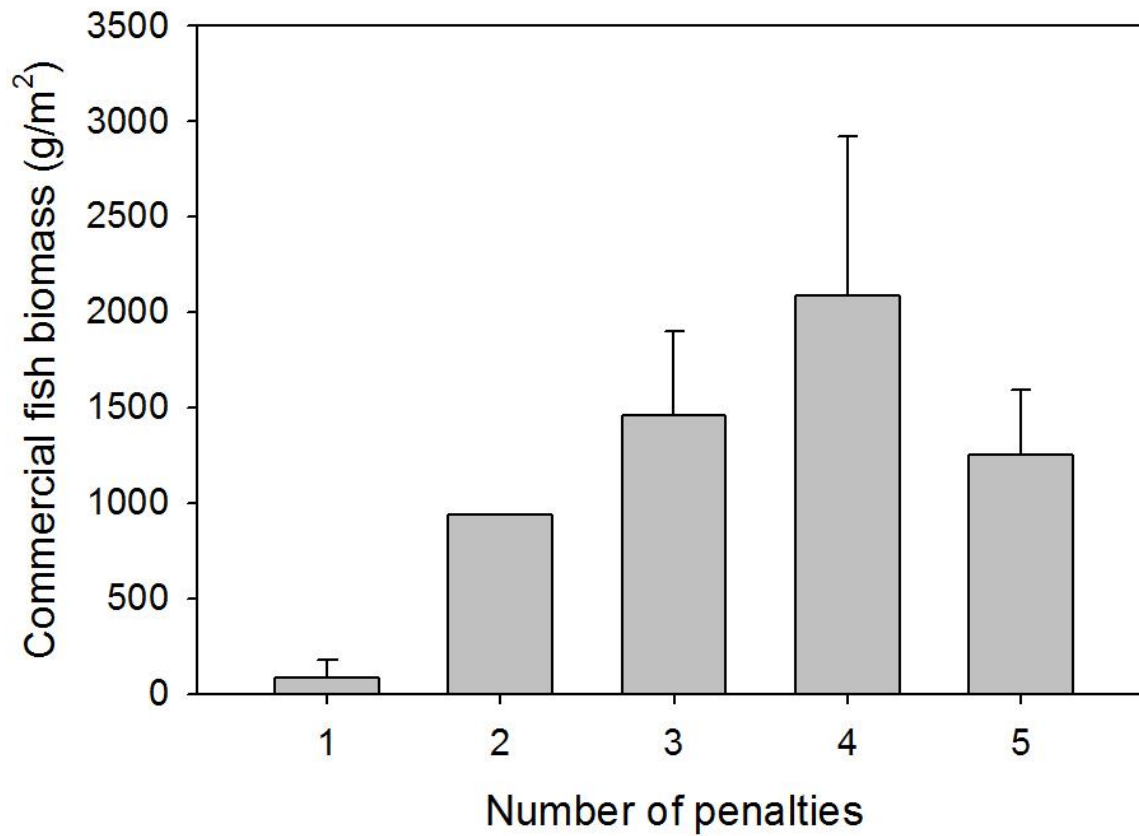


Figure 1.5. Commercial fish biomass (g/m<sup>2</sup>) in MPAs with varying numbers of penalties used for enforcement of MPA regulations (ANOVA  $F_{4,111}=2.279$ ,  $p=0.07$ ). Error bars= 95% CI. Only one site in one MPA used two penalties.

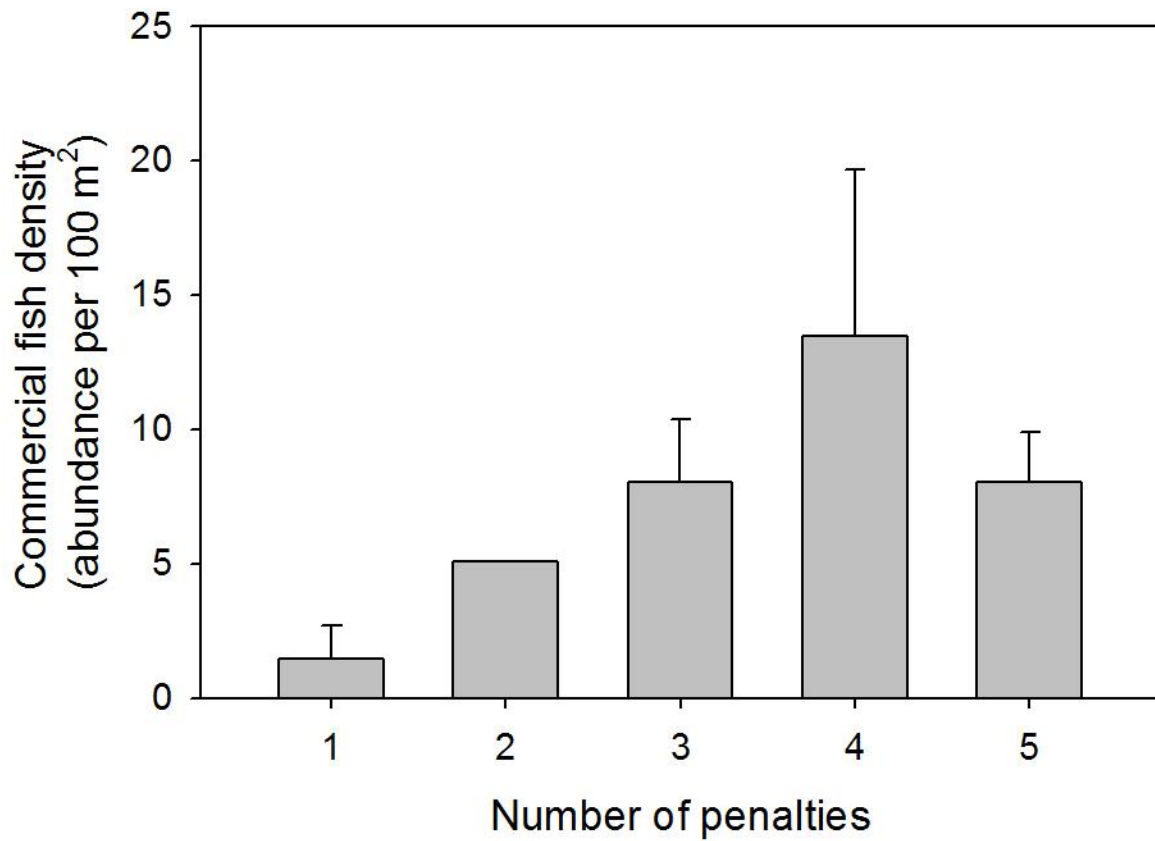


Figure 1.6. Commercial fish density (abundance/ 100 m<sup>2</sup>) in MPAs with varying numbers of penalties used for enforcement of MPA regulations (ANOVA  $F_{4,111} = 2.101$ ,  $p = 0.09$ ). Error bars = 95% CI. Only one site in one MPA used two penalties.

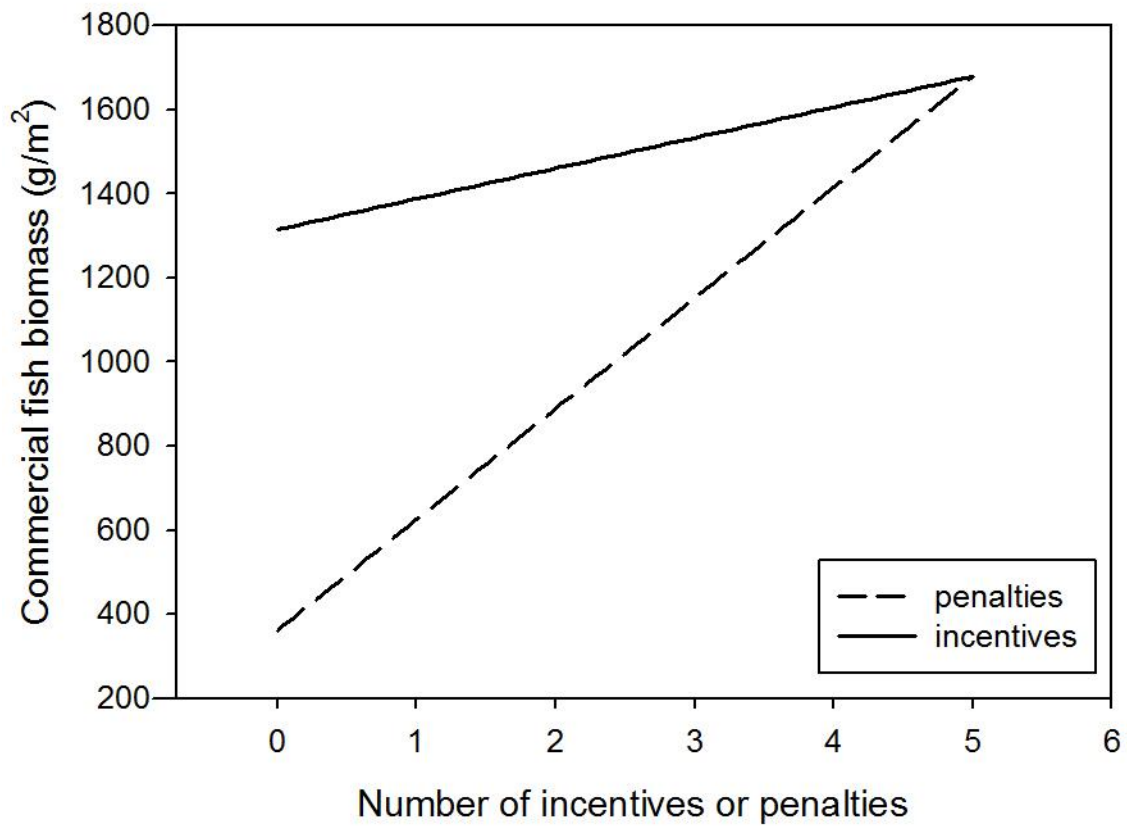


Figure 1.7. Interaction between penalties and incentives (ANOVA,  $F_{4,118}=4.305$ ,  $p=0.003$ ).

Table 1.2. Results from multi-linear regression analyses of types of incentives correlated to different ecological indicators, with coefficients of predictors that improved model fit ( $\Delta AIC > 2$ ) and level of significance: \*  $p < 0.05$ ; \*\*  $p < 0.01$ ; \*\*\*  $p < 0.001$

Incentive	Total fish biomass	Commercial fish biomass	Herbivore fish biomass	Piscivore fish biomass	Parrot fish biomass	Percent coral cover
Environmental Education						-11.418*
Skills training		816.8*		548**		
Exchange of Equipment	-9602.4***	-1102.1**	-1813*	-784.1**	-2298***	-6.309*
Purchase of Equipment	6607.9**				1354***	
Employment						
Other		1509.2*				

For example, percent coral cover negatively correlated to environmental education and all ecological indicators negatively correlated with the incentive exchange of equipment (Table 1.2). However, skills training positively correlated to commercial fish biomass and piscivore fish biomass, while purchase of equipment positively correlated to total fish biomass and parrot fish biomass and the category other correlated positively to commercial fish biomass. Additionally the variogram demonstrated no spatial auto-correlation in commercial fish biomass or density across the sites utilized in this study.

## **4. Discussion**

### *4.1 Relationship between governance strategies and ecological condition*

Our multi-country comparison demonstrates correlations between ecological indicators and governance strategies used to promote regulatory compliance across Caribbean MPAs. MPAs that prohibit harvest of marine life hosted greater biomass of commercial fish species, indicating marine reserves are effective in conserving target species (Figure 1.2). Commercial fish biomass and density increased with an increasing number of both penalties and incentives used to encourage compliance with MPA regulations (Figures 1.3-1.7). The results suggest that the sustainable use of marine resources is correlated to governance strategies used to promote compliance and that having penalties and incentives present as a governance strategy may be a key attribute of MPAs that are successful in maintaining high levels of commercial fish biomass and density (Pollnac et al. 2010; Edgar et al. 2014). This finding also suggests that methods used to encourage compliance with MPA regulations that combine both penalties and incentives can aid in the protection of fishery resources. Although MPAs have traditionally focused more

heavily on penalties to enforce compliance (Crawford et al. 2004), the positive relationship between increasing the number of incentives with commercial fish biomass and density observed in this study suggests that incentives may help form successful enforcement strategies.

Consistent with previous governance studies (Jones et al. 2013; Jones 2014a) interactions among incentives can lead to governance systems that are more resilient in protecting marine areas from anthropogenic and natural perturbations. A diversity of governance mechanisms designed to promote compliance with MPA regulations may be necessary to achieving MPA objectives (Gutiérrez et al. 2011; Jones 2014a).

Alternatively, the higher number of penalties and incentives correlating to greater fish biomass and density may be more indicative of greater state capacity and political will present in these MPAs rather than being attributed solely to the presence of penalties and incentives. Previous studies have shown that greater state capacity, political will, social capital and leadership leads to a greater resilience of governance structures and the ability of MPAs to achieve conservation objectives (Gutiérrez et al. 2011; Jones et al. 2013; Jones 2014a). The results from this study are intended to explore connections between ecological indicators and governance attributes across multiple countries and management regimes. The data suggest that having regulatory mechanisms that employ penalties and incentives have the potential for leading to greater density and biomass of commercial species, though as a highly correlative study firm conclusions as to the degree of efficacy of these strategies will need further investigation on the state capacity of the governance systems analyzed and the degree to which these specific strategies are enforced. Additionally, other studies have demonstrated the importance of oceanographic features in driving species distributions (Chollett et al. 2012), which were not analyzed in this study; however the lack of spatial auto-correlation in

commercial fish biomass and density suggests that these factors may not be the dominant drivers of the observed differences. Commercial fish biomass demonstrated a positive trend with incentives and penalties while there was no trend in total fish biomass suggesting that the impact of governance systems is greatest upon species whose harvest is governed by the resource use regulations.

The influence of penalties on commercial fish biomass and density were both marginally significant (Figure 1.5,  $p=0.065$  and Figure 1.6,  $p=0.086$ , respectively). It is necessary to note that our data set had a relatively low sample size in terms of sites with ecological data in MPAs with less than three penalties ( $N=4$ , Total  $N=132$ ). Therefore, MPAs that employ at least three penalties with incentives to promote compliance tend to host greater biomass and density of commercial species (Figures 1.3-1.7). Alternatively, the data may also indicate that sites with greater biomass and density of commercial fish species may increase the likelihood that governance systems are stronger. Since these areas have more commercial fish biomass and density, governance systems to protect these resources may have been put in place due their economic importance. This study only focuses on correlations between governance of enforcement strategies and ecological condition, thus future research should also examine before-after-control experimental designs to fully determine casual relationships in MPA performance. Additionally, overall our sample size of 21 MPAs is relatively small and greater contrast in the incentives and penalties may be observed with a larger sample size.

#### *4.2 The importance of incentives*

An interaction effect between the presence of incentives and penalties on commercial fish biomass was indicated, which suggests that the use of both penalties and incentives has greater efficacy in conjunction than using either penalties or incentives alone (Figure 1.7). This finding



is consistent with other studies that have suggested redundancy of management tactics and stronger governance institutions in general lead to more successful fisheries management (Gutiérrez et al. 2011; Jones et al. 2013; Jones 2014a). Additionally, providing a conjunction of economic, participatory and knowledge-based incentives provide further support that incentives can be useful in changing behavior of resource users toward promoting conservation objectives (Nur et al. 2001; Grafton et al. 2006; Jones et al. 2013; Jones 2014a). In this study economic incentives were assessed in terms of purchase of fishing equipment, sometimes known as buybacks or decommissioning schemes, which positively correlated to total fish biomass and parrot-fish biomass (Table 2). Buybacks can help promote conservation objectives if coupled with other economic incentives and can restructure relations among fishers as well as change fisher behavior (Guyader et al. 2004; Squires 2010). Additionally one participatory incentive addressed in this study includes employment though this incentive did not positively correlate to any indicators (Table 1.2). Participatory incentives such as including resource users in the process of MPA management and decision-making have been shown to promote sustainable resource use in some cases (Basurto 2005b, 2008; Ostrom 2009; Basurto & Coleman 2010; Gutiérrez et al. 2011), though the efficacy of these strategies may be context dependent. Interpretative incentives such as environmental education negatively correlated to coral cover, while skills training positively correlated to commercial fish biomass and piscivore fish biomass (Table 1.2). Interpretative incentives such as public communication, education and awareness on the significance and susceptibility of marine ecosystems to anthropogenic and natural threats can form key components of management and outreach strategies (Petrosillo et al. 2007; Leisher et al. 2012; Jones et al. 2013). Also promoting awareness of MPA regulations and restrictions has been demonstrated to promote compliance with regulations (McCay & Jones 2011; Leisher et al.

2012; Jones et al. 2013). The results from individual incentive types should be interpreted with caution due to the small sample size and the possibility for random correlations that are not necessarily indicative of larger impacts of policy. For example, the incentive exchange of equipment unexpectedly correlated negatively to ecological indicators (Table 1.2). Nonetheless, specific types of incentives may more strongly influence compliance behavior than others. Thus, future studies may include a more fine scale analysis of specific penalty and incentive types for promoting compliance including behavioral surveys of fishers to determine how fisher behavior is influenced by specific penalties and incentives.

Since transaction costs for enforcing penalties in MPA regulations is high, incentives can provide added efficacy at lower cost (Hutton & Leader-Williams 2003). The management costs need to be reasonable compared to the economic output obtained from marine resources for successful MPA administration (Raakjær Nielsen 2003). Due to the limits in the amount of resources management institutions can devote to enforcement activities an objective is to strike a balance between the costs of enforcement activities and profit to be obtained from marine resource extraction (Raakjær Nielsen 2003). In addition, an incentive-based approach may diminish the opportunity cost of compliance for fishers who may now receive added benefits for complying with the regulations (Grafton et al. 2006; Gjertsen & Niesten 2010). Incentive-driven conservation can promote sustainable resource use in the context of protected area management providing there is support on a local level (Wells & McShane 2004). Incentives appear to be overlooked in many governance strategies designed to promote compliance, though our analysis suggests that their inclusion may help ensure sustainable resource use.

## **5. Conclusions**

Marine protected areas have become a crucial strategy for conservation of sensitive

marine ecosystems, particularly in developing countries. A precondition for the sustainable and efficient management of marine resources is that the imposed regulations can be controlled and enforced (Raakjær Nielsen 2003). However, the transaction costs for enforcing regulations in MPAs, particularly in the developing world, are particularly high due to features such as high resource mobility, unpredictable system dynamics, and the large size of the resource system (Ostrom 2009; Gutiérrez et al. 2011). An added return on efficacy of regulations may be achieved through the use of incentives with relatively low investment as compared to the investment required to monitor and penalize users for violating regulations. The opportunity cost of abiding by regulations can be reduced by providing incentives (Grafton et al. 2006; Gjertsen & Niesten 2010), since fishers may experience gains by abiding by regulations. Fisher perceptions of both the regulatory process and its outcomes are drivers for compliance behavior, and their perceptions of fairness and treatment by enforcement authorities matters (Alder et al. 1994; Hønneland 2000; Viteri & Chávez 2007). Incentives that better support and empower fishers and their livelihoods may be the crux of a successful MPA program (Nur et al. 2001; Basurto 2008; Basurto & Coleman 2010).

Our study indicates that the cumulative impact of an increasing number of incentives and penalties is correlated to greater biomass and densities of commercial fish species, which suggests that a conjunction of multiple incentives and penalties is the optimal strategy for enforcing regulations in MPAs (Jones et al. 2013). More research assessing the impacts of incentives-based approaches to promote compliance with marine protected areas can help reduce uncertainty and achieve optimal governance strategies for compliance with regulations. The results of this study are correlative and useful in analyzing multiple countries and multiple management regimes, however comprehensive before-after-control- intervention impact

evaluations of MPAs coupled with qualitative studies are necessary to reinforce the results of this study. Nonetheless our findings of the positive correlation between the use of incentives and penalties in MPAs with higher commercial fish biomass and density provide insight for decision makers to develop strategies to improve management of their MPA by recognizing the importance of both incentive and penalty-based methods used to promote compliance with regulations.

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## CHAPTER 2

### THE DISTRIBUTION OF THE INVASIVE TUNICATE *DIDEMNUM VEXILLUM* IN ATLANTIC SEA SCALLOP HABITAT *PLACOPECTEN MAGELLANICUS* HABITAT ON FISHING GROUNDS AND CLOSED AREAS OF GEORGES BANK

#### **Abstract**

An invasive colonial tunicate (*Didemnum vexillum*) was initially observed on Georges Bank in 1998, and it has since spread in benthic environments on fishing grounds and areas closed to bottom-fishing. It can form dense mats on gravel substrates that are also a preferred habitat for the Atlantic sea scallop (*Placopecten magellanicus*), which supports one of the most valuable commercial fisheries in the United States. We used HabCam, a vessel-towed underwater imaging system, to investigate the spatial distributions of *P. magellanicus* and *D. vexillum* in a region that includes fishing grounds and an area protected from bottom-fishing. We found a negative relationship between *P. magellanicus* and *D. vexillum*, after controlling for substrate and management status, suggesting that *D. vexillum* competes for habitat with *P. magellanicus*. We also applied the geostatistical method of universal kriging to interpolate the distribution of *D. vexillum* based on the covariables gravel, depth and area. Our results indicate that *D. vexillum* is more common in areas open to fishing than in the areas closed to fishing, after taking bottom substrate effects into account. *Didemnum vexillum* appears to have spread over large portions of the northern edge of Georges Bank. This research evaluates essential fish and invertebrate habitat degradation caused by an invasive species.

## 1. INTRODUCTION

Marine invasive species are a major threat to biodiversity, since once they are established, eradication is unlikely and the interaction with existing communities modifies native habitats (Bax et al. 2003; Glasby et al. 2005; Coutts & Forrest 2007; Molnar et al. 2008; Smith et al. 2014). Habitat modification by invasive species can interact synergistically with other drivers of environmental change such as global climate change, thereby exacerbating effects on native species (Didham et al. 2007; Hellmann et al. 2008; Rahel & Olden 2008). Marine invasions most frequently occur through ballast water, since at any given 24 hour period between 3,000 and 10,000 different species are being transported between bio-geographic regions in ballast tanks alone (Carlton 2001; Wasson et al. 2001). Additionally non-indigenous marine species also spread through hull fouling of commercial shipping and recreational vessels, aquaculture, fishing equipment, and the aquarium trade (Relini et al. 2000; Bax et al. 2003; Daley & Scavia 2008; Herborg et al. 2009; Acosta & Forrest 2009). The rate at which foreign organisms are establishing in ports has increased dramatically due to human-mediated activities (Molnar et al. 2008). Marine invasive species can have negative impacts on human health and decrease economic productivity from resources such as fisheries, aquaculture, and tourism (Lovell & Stone 2005; Williams & Grosholz 2008; Molnar et al. 2008; Vilà et al. 2010).

The invasive sea squirt *Didemnum vexillum*, originating from Japan (Stefaniak et al. 2012), was first observed on Georges Bank in 1998 (Bullard et al. 2007). *D. vexillum* has colonized at least 230 km<sup>2</sup> of pebble/gravel habitat in Georges Bank leading to

concerns about the impact this species may have on valuable fishery resources (Valentine et al. 2007b). It has several characteristics that contribute to its ability to invade, such as early maturation, rapid colony growth as a result of asexual budding, ease of attachment to firm substrates, toleration of a wide temperature range and the ability to spread by colony fragmentation as well the lack of natural predators in the region (Valentine et al. 2007a; Carman et al. 2009, 2014; Lambert 2009; Stefaniak et al. 2012; Stefaniak & Whitlatch 2014). *Didemnum vexillum* may also prevent other benthic organisms from settling and growing on colony surfaces by sequestering acidic and organic allelopathic compounds in their tunics (Valentine et al. 2007a; Carman et al. 2009). In particular, scallop spat cannot settle on *D. vexillum* colonies (Morris et al. 2009) and *D. vexillum* also can interfere with scallop swimming (Dijkstra & Nolan 2011). Additionally, *D. vexillum* can thrive on gravel substrate that the Atlantic sea scallop (*Placopecten magellanicus*) prefers; thus *D. vexillum* may be able to reduce the habitat available to sea scallops and thereby reduce the overall abundance of scallops. Furthermore, *D. vexillum* can also colonize the upper valve of adult scallops and other bivalves, which may affect their ability to feed (Valentine et al. 2007a; Carman et al. 2009). Thus, *D. vexillum* exhibits a number of characteristics that allow it to successfully outcompete other benthic epifaunal and macrofaunal species for limited space. All of these traits combine to make it a threat to benthic marine habitats and fisheries in the area.

Colonies of *D. vexillum* on Georges Bank appear as thin encrusting layers or produce tendrils that protrude from thick encrusting mats. It can reproduce both sexually and asexually by budding as well as fragmentation (Carman et al. 2014). Larvae from sexual reproduction swim for a few hours before attaching to substrate and



metamorphosing. However, asexual reproduction and fragmentation are probably responsible for the majority of the spread of this species (Lengyel, et al. 2009). *D. vexillum* has become a concern as a nuisance species because it reproduces rapidly, has a long breeding season, fouls ship's hulls and maritime structures, and can invade productive marine habitats such as shellfish aquaculture sites and fishing grounds (Valentine et al. 2007a; Daley & Scavia 2008; Carman et al. 2009).

Various methods have been suggested to control the impacts of marine invasive species including chemical, mechanical, and biological control options (Thresher & Kuris 2004; Coutts & Forrest 2007; Switzer et al. 2011). Since biological control may be effective in some cases (Lafferty & Kuris 1996; Mumby et al. 2011), there is interest in the broader possibilities to manage invaders in the oceans. Biological control has successfully regulated pest populations in terrestrial agroecosystems, however for marine environments, host specificity frequently cannot be guaranteed and thus this practice is riskier than on land (Secord 2003). Additionally, chemical and mechanical control of non-indigenous ascidians has been successful in some cases though implementation may be difficult or impossible to maintain when applied to large areas in natural environments (Coutts & Forrest 2007; Switzer et al. 2011). The challenge of managing marine invasive species will require bridging gaps between science and policy to develop an adaptive decision making framework that makes use of information systems (Thresher & Kuris 2004; Williams & Grosholz 2008; Olenin et al. 2014; Faulkner et al. 2014).

The Atlantic sea scallop (*P. magellanicus*) is a benthic bivalve mollusk that supports one of the highest valued fisheries in the United States, with total revenues reaching almost \$500 million in 2013 (Lowther & Liddel 2014). This fishery has

recovered from a near collapsed state in the mid-1990s using a combination of conventional management measures such as effort control and gear regulations together with rotational and long-term closed areas (Hart & Rago 2006). In particular, three areas on or near Georges Bank were closed to groundfish and scallop fishing in December 1994 (Murawski et al. 2000, Figure 2.1). Sea scallop biomass inside these closures increased over 20-fold between 1994 and 2004; scallop biomass in these areas has subsequently declined somewhat after portions of these areas were reopened to fishing (Hart & Rago 2006; Hart et al. 2013).

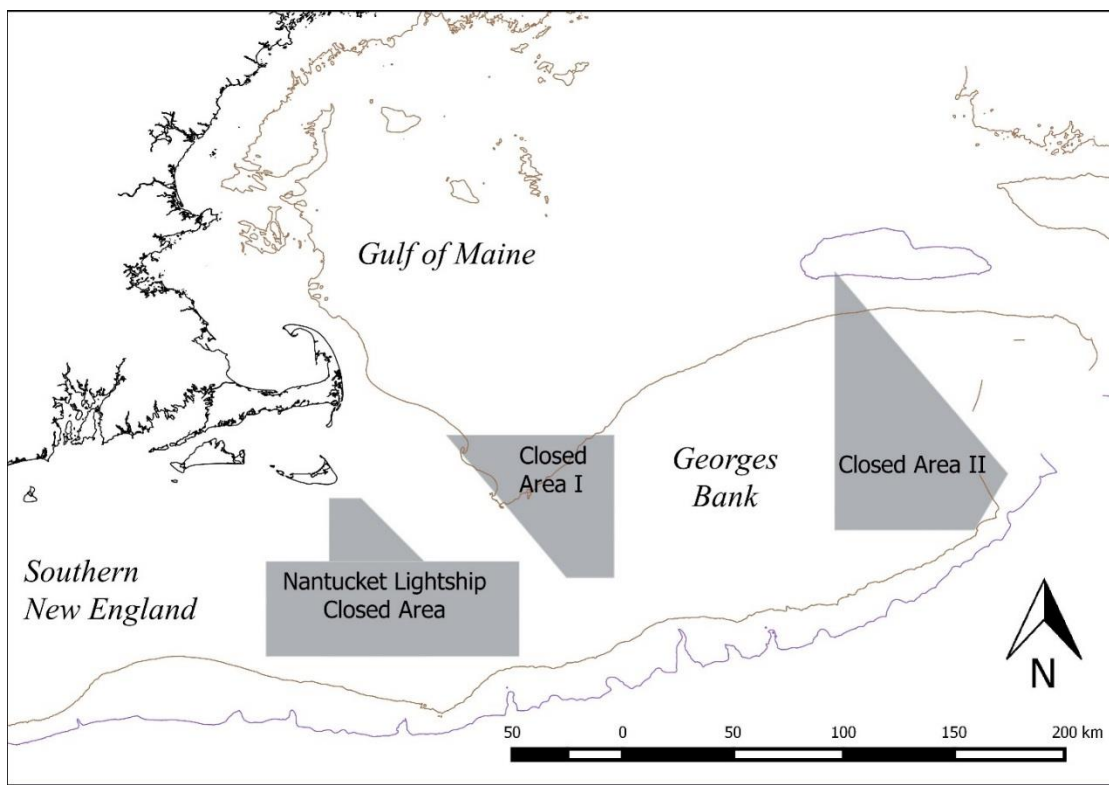


Figure 2.1. Georges Bank, with closed areas.

In this study we evaluated the distribution of the invasive tunicate *D.vexillum* in Atlantic sea scallop habitat. We used the habitat camera mapping system (HabCam), a vessel-towed underwater camera system, to explore the spatial distribution of sea scallops and *D. vexillum* in areas protected and unprotected from bottom-fishing on Georges Bank to test if sea scallops are negatively related with this invasive species. Additionally, we evaluated if *D.vexillum* spread is greater in areas open or closed to bottom-fishing. We also applied geostatistical techniques such as ordinary and universal kriging to determine the spatial distribution of *D.vexillum* cover across the entire study area. Georges Bank provides an important opportunity to determine how bottom fishing affects interactions in the benthic community because it is well monitored and substantial portions have been closed to bottom fishing since 1994. Activities such as scallop dredging and bottom trawling may have the potential to facilitate the spread of the invasive *D. vexillum* as a result of increased colony fragmentation (Morris & Carman 2012), or the disturbance from bottom-fishing may open space for *D. vexillum* to colonize. We hypothesize that there will be a negative relationship between sea scallops and *D. vexillum*. This hypothesis is based on the literature that has demonstrated the tunicate's ability to prevent settlement of scallop spat and perhaps also increase mortality of adults (Morris et al. 2009). We also hypothesize that areas open to fishing will have greater cover of the invasive *D. vexillum* due to greater rates of disturbance and possibly also fragmentation of colonies from contact with fishing gear. This work can further our understanding of invasive species effects and how species interactions may affect habitat for fishery resources. Finally, possible management actions designed to mollify the negative impacts of the invasive *D. vexillum* on essential fish and invertebrate habitat are

discussed.

## 2. METHODS:

### 2.1 Study area

Georges Bank is a shallow, highly productive, submerged plateau off the coast of New England that supports a number of valuable commercial fisheries (Butman & Beardsley 1987). Surficial sediments of Georges Bank are dominated by large expanses of sand substrate interspersed with gravel and gravel/sand regions that mainly occur on its northern and western portions (Twichell et al. 1987). Interspersed within the gravel regions are large glacial erratics and boulders that can provide refuge sites for a diverse assemblage of organisms. The study site is located in the northeastern portion of Georges Bank, in the area bounded between  $41^{\circ} 49'$  N and the northern edge of the bank, the Hague line dividing the U.S. and Canadian E.E.Z. on the east, and a boundary parallel to the Hague line on the west (Figure 2.2a). The portion to the west of  $67^{\circ} 20'$  W is open to fishing, while the portion to the east has been closed to all groundfish and scallop gear since December 1994, and is a part of Closed Area II. This area contains both sand and gravel substrates as well as high densities of sea scallops and *D. vexillum* in some locations (Figure 2.2).

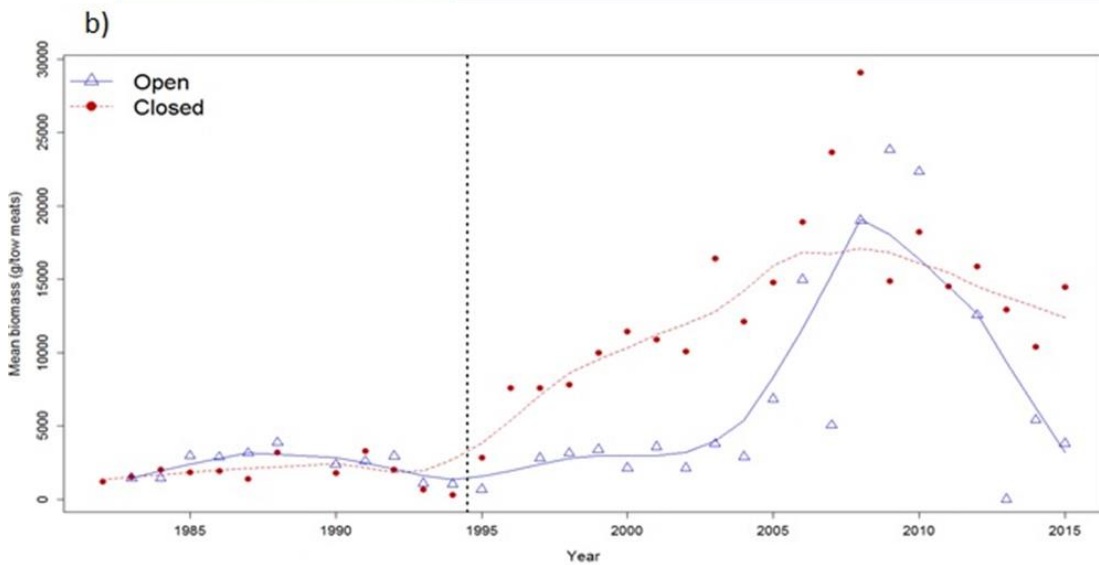
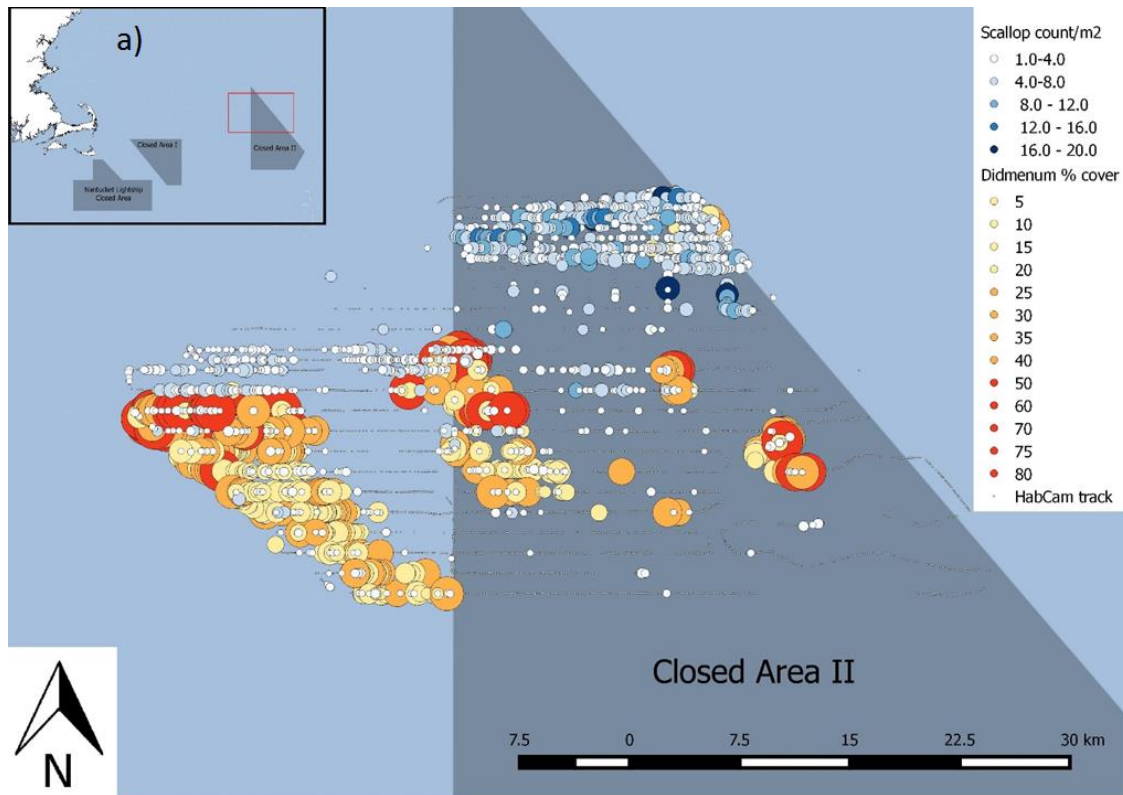


Figure 2.2 (a) Chart of HabCam survey with scallop density (counts/m<sup>2</sup>) and *D. vexillum* percent cover. Size of data points scaled by density and percent cover. (b) Mean scallop biomass in the open and closed portions of the study area, 1982-2016, from the NEFSC scallop dredge survey (Hart & Rago 2006). The lines are lowess smoothers with stiffness

of 0.25. The closed areas were put in place in December, 1994 (dotted vertical line).

## **2.2 Data collection**

Data for this project was collected from HabCam v2, a high resolution imaging system that provides visual surveys of benthic marine organisms without disturbing the habitat itself (Howland et al. 2006; Taylor et al. 2008; York et al. 2008). These data can be used to evaluate physical features of the environment that drive spatial and temporal variability of benthic fisheries such as the Atlantic sea scallop. The HabCam v2 vehicle is towed at speeds of 5-6 knots during which it collects data at a rate of about six images per second providing a continuous band of data input along the survey track. The equipment on HabCam v2 includes a digital still camera (UNIQ Vision, Inc. UP-1800-CL), four machine vision strobes (Perkin Elmer MVS-5000) mounted in underwater housings placed radially around the camera 50 cm apart. Other sensors on HabCam v2 include a CTD (SBE 37-IS MicroCat, Seabird electronics Inc.) for conductivity and temperature measurements, a YSI 6600 Sonde multiparameter sensor, and a Benthos altimeter (PSA-916), which measures distance from the vehicle to the bottom. The data for this project were collected on the F/V Kathy Marie by HabCam v2 in July of 2012 in and to the west of the northern portion of Closed Area II (Figure 2.2a). We also present the long-term sea scallop biomasses in the open and closed portions of the study area, based on the National Marine Fisheries Service Northeast Fisheries Science Center (NMFS-NEFSC) scallop dredge survey to help understand the effects of the closure on sea scallops prior to the invasion of *D. vexillum* (Figure 2.2b). These data have been collected since 1982 using a modified 2.44m New Bedford-style scallop dredge as the sampling gear; see (Hart & Rago 2006) for more details on this survey. A lowess smoother (stiffness = 0.25)

was used to smooth the dredge survey time series trend.

### **2.3 Data processing:**

HabCam images were annotated to identify members of the invertebrate community, which were identified to the lowest taxonomic group possible for one in every 200 images collected by HabCam v2 during the July 2012 survey. In total 5,309 images were annotated for members of the invertebrate community both in and adjacent to Closed Area II (Figure 2.2). All images used in the study were annotated by the same annotator (K.H.).

Scallops were separated into recruits (less than or equal to 75 mm shell height) and adults (greater than 75mm shell height) based on shell height. Locations were identified as being inside or outside of the closed area using the intersect and difference geoprocessing tools in Quantum GIS (QGIS development team 2015), and these were subsequently separated for analyses. Density estimates for scallops were obtained by dividing species counts by the area of the field of view for each image. Sediment type was evaluated visually based on the fraction of the image covered. *D. vexillum* percent cover was also evaluated based on visual estimates of the fraction of the image that it covers. Sediment composition and *D.vexillum* percent covers were estimated based on 5% increments.

### **2.4 Data analysis:**

#### *Modeling the relationship between D. vexillum and scallop distributions*

The effects of *D. vexillum* on adult and recruit scallop populations were analyzed using generalized linear models (GLM), generalized additive models (GAMs), non-linear least squares (NLS) as a result of the non-linear nature of the relationship observed. Model fits from generalized additive models were selected based on lowest AIC. In order to reduce

localized effects and issues with sample auto-correlation data for adult and recruit scallops, *D. vexillum* and proportional gravel cover were first averaged based on approximately over 10 image blocks, covering approximately 1 km. Over-dispersion was detected in the scallop data; therefore a (quasi-)Poisson family was used in the GAM, in which the variance is given by  $\Phi * \mu$ , where  $\mu$  is the mean density and  $\Phi$  is the dispersion parameter, thus allowing variance to be greater than the mean. Gravel substrate and protected area (open/closed to fishing) were used as a covariate and factor respectively in the GAMs to isolate the influence of *D. vexillum* on adult and recruit scallop distributions according to the formula:

scallop density  $\sim s(D. \textit{vexillum}) + c * \text{factor}(\text{Open/Closed}) + s(\text{proportional gravel cover}) + \epsilon$

where  $s$  represents a spline smoother,  $c$  is an estimated parameter, and  $\epsilon$  is an error term.

Temperature was also considered in all models, but not found as a significant predictor of scallop density thus it was eliminated as a predictor variable.

#### *Determining the effect of the closed area on scallops and D. vexillum*

The influence of the area closed to bottom-fishing on adult and recruit scallop density, and *D. vexillum* proportional cover from HabCam data were analyzed using analysis of covariance (ANCOVA) with the proportional cover of gravel substrate as a covariate, since both *P. magellanicus* and *D. vexillum* are most abundant on gravel substrate. Collinearity was observed between the two most dominant substrate types, gravel and sand (adjusted  $R^2=0.875$ ), and hence only gravel was used as a covariate in the analyses. The effect of protected area on mean density of adult sea scallops, recruit scallops and *D. vexillum* proportional cover with greater than or equal to 50% gravel substrate represented as “high gravel” and below 50% is represented as “low gravel” shown in



Figure 2.4.

*Interpolating Didemnum vexillum distribution across the study area using geostatistics*

The distribution of *D.vexillum* was modeled by universal kriging with gravel, depth and the categorical variable region, representing whether a point was inside or outside the closed area, as covariables using the R package gstat and sp (Pembesa, E.J. 2004; Bivand et al. 2013). The universal kriging geostatistical approach results in the best linear unbiased estimates of the parameters and optimally weights each sample observation prediction (Cressie 1993). A 100x100 grid was created for the study area to interpolate over using the spatial structure in conjunction with gravel, depth and area covariables. Gravel and depth were each spatially interpolated using ordinary kriging to provide input into the spatial linear model for predicting the proportional cover of *D.vexillum* (S1 Appendix). The exponential model was used to fit the variogram for both gravel and depth (S1 Appendix). The kriged estimates for depth and gravel were then used to create the prediction grid (S2 Appendix). Once this grid was created, gridded points were identified as being in Closed Area II or the region open to fishing and region was added as a grid co-variable (QGIS development team 2015). A variogram was fit with a spherical model of the residuals from the linear regression with the covariates gravel and depth and the categorical predictor variable region (Figure 3). The universal kriging model applies the following equation where our interpolated value for *D.vexillum* ( $Z$ ) is based on the covariables, gravel, depth and region and the variance-covariance matrix ( $\eta$ ):

$$Z = \alpha(\text{gravel}) + \beta(\text{depth}) + \gamma(\text{region}) + \eta$$

Where  $\eta \sim MVN(0, \Sigma)$

This model is then used to demonstrate the interpolated density of *D.vexillum* infestation over the entire study area.

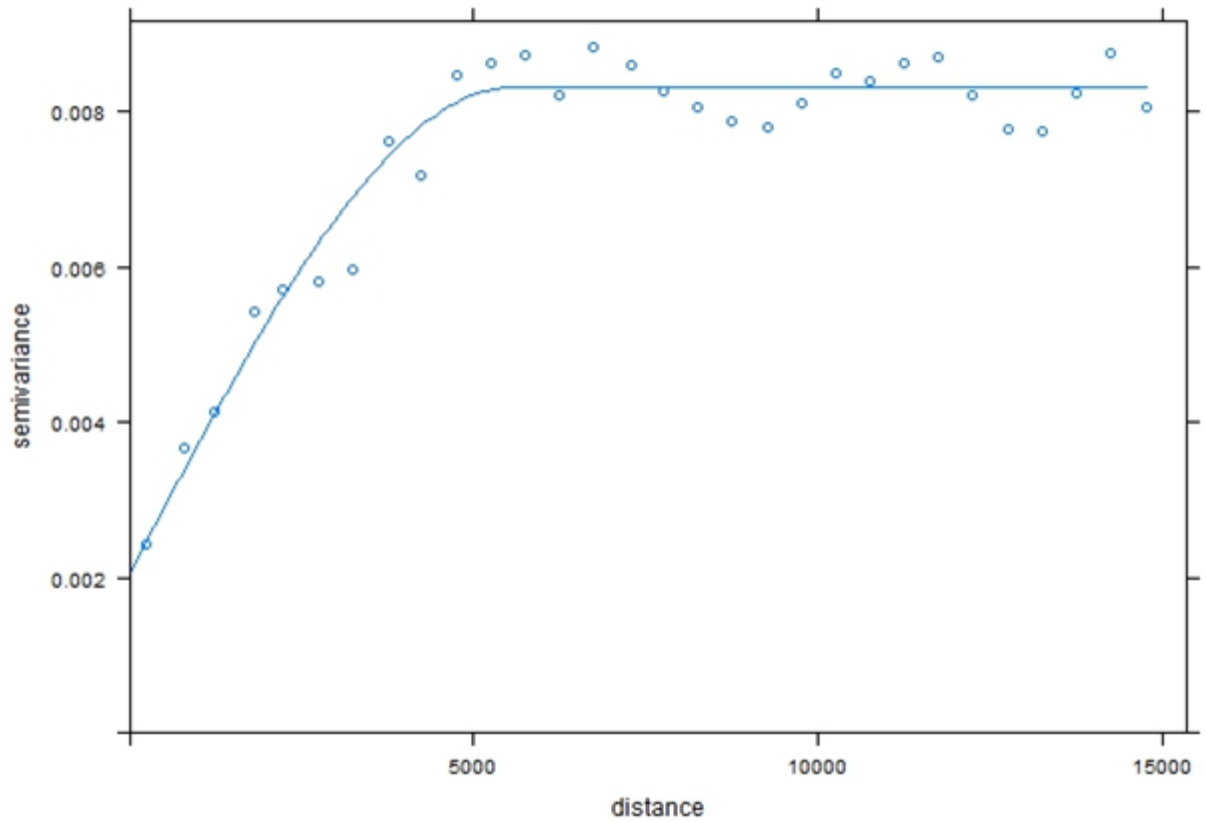


Figure 2.3. Variogram model with spherical fit for *D.vexillum* using co-variables: gravel, depth and area.

### 3. RESULTS:

#### **3.1 Interaction between scallops and *D. vexillum***

The relationship between adult scallops and *D. vexillum*, and recruit scallops and *D. vexillum* was modeled using generalized additive models due to the non-linear relationship observed (Figure 2.4, Table 2.1). Since both the substrate and region (i.e. open or closed to bottom-fishing), were found to significantly influence the densities of scallops and *D. vexillum*, gravel substrate and region were included in both adult and recruit models as a covariate and factor, respectively (Table 2.1, Figure 2.4). The relationship for adult scallop density and *D. vexillum* essentially follows an exponential decline function with increasing *D. vexillum*; recruit scallop density showed a similar relationship. Model predictions were made holding gravel substrate at the mean level from all sites to isolate the influence of *D. vexillum* on scallop density (Figure 2.4). At higher *D. vexillum* densities, the mean predicted recruit density also increased slightly (Figure 2.4b), but this is likely an artifact since there are few data points supporting this prediction as reflected by the increasingly large confidence intervals (N=20 for recruits in areas with greater than 0.15 proportional *D. vexillum* cover, as compared to a total N=530).

Table 2.1. Interaction between adult and recruit sea scallops with *D. vexillum* using generalized additive models p<0.05\*,p<0.01\*\*,p<0.001\*\*\*

Response variable	<i>D. vexillum</i>	Area (SE)	gravel
Adult density Deviance explained =53.6% Distribution: Poisson	***	-0.819 *** (0.128)	***
Recruit density Deviance explained= 48.2% Distribution: Poisson	***	-0.214* (0.095)	***

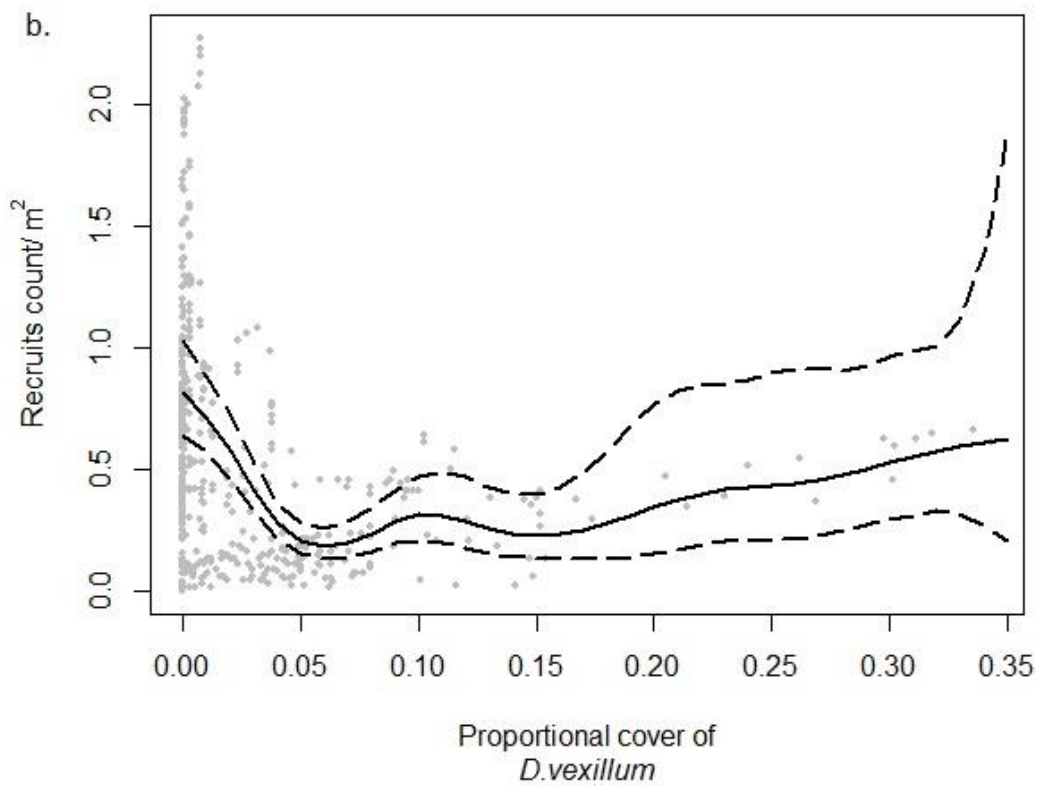
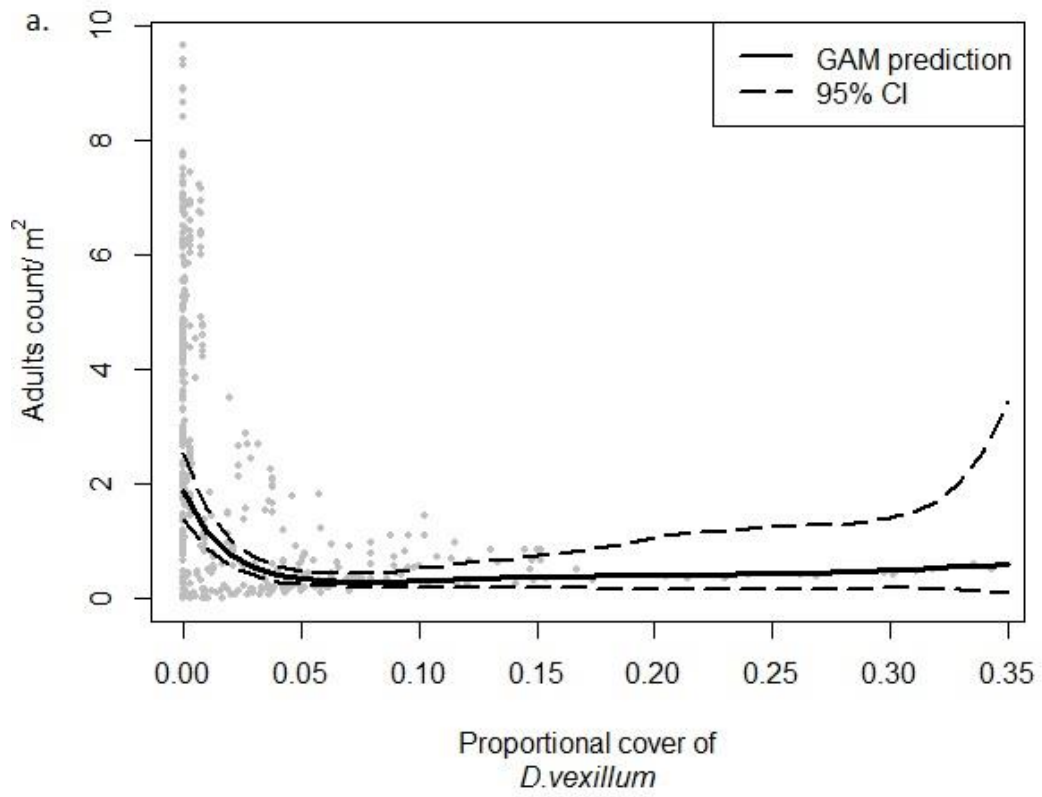


Figure 2.4. a. Prediction of adult scallop density from the generalized additive model response to *D. vexillum* proportional cover with gravel substrate held at its mean value in both open and closed areas shown with 95% confidence intervals. b. Prediction of recruit scallop density from the generalized additive model response to *D. vexillum* proportional cover with gravel substrate held at its mean value in both open and closed areas with 95% confidence intervals.

### **3.2 The effect of the closed area on scallops and *D. vexillum***

Adult sea scallop density was significantly greater in the areas closed to bottom-fishing and positively correlated with gravel substrate, with a significant interaction between the two (ANCOVA, Region:  $F_{1,526} = 99.87$ ,  $p < 0.001$ ; covariate gravel estimate: 4.31,  $F_{1,526} = 41.34$ ,  $p < 0.001$ ; interaction:  $F_{1,526} = 5.59$ ,  $p < 0.05$ , Figure 2.5a). Recruits were not significantly greater in the region closed to bottom-fishing ( $F_{1,526} = 0.24$ ,  $p > 0.05$ ), however recruit density was positively associated to gravel substrates (gravel covariate estimate = 1.20,  $F_{1,526} = 131.37$ ,  $p < 0.001$ ; interaction not significant:  $F_{1,526} = 0.24$ ,  $p > 0.05$ , Figure 2.5b). Proportional cover of *D. vexillum* was significantly greater in the regions open to bottom-fishing and positively associated to gravel substrate (ANCOVA; Region:  $F_{1,526} = 89.49$ ,  $p < 0.001$ ; covariate gravel estimate: 0.06;  $F_{1,526} = 28.24$ ,  $p < 0.001$ ; interaction not significant:  $F_{1,526} = 0.13$ ,  $p > 0.05$ , Figure 2.5c). Additionally, the time series of the dredge survey (1982-2015) for scallop biomass also demonstrates the efficacy of the closed areas over time as evidenced by the increase in scallop biomass inside the protected area after it was closed in 1994 (Figure 2.2b).

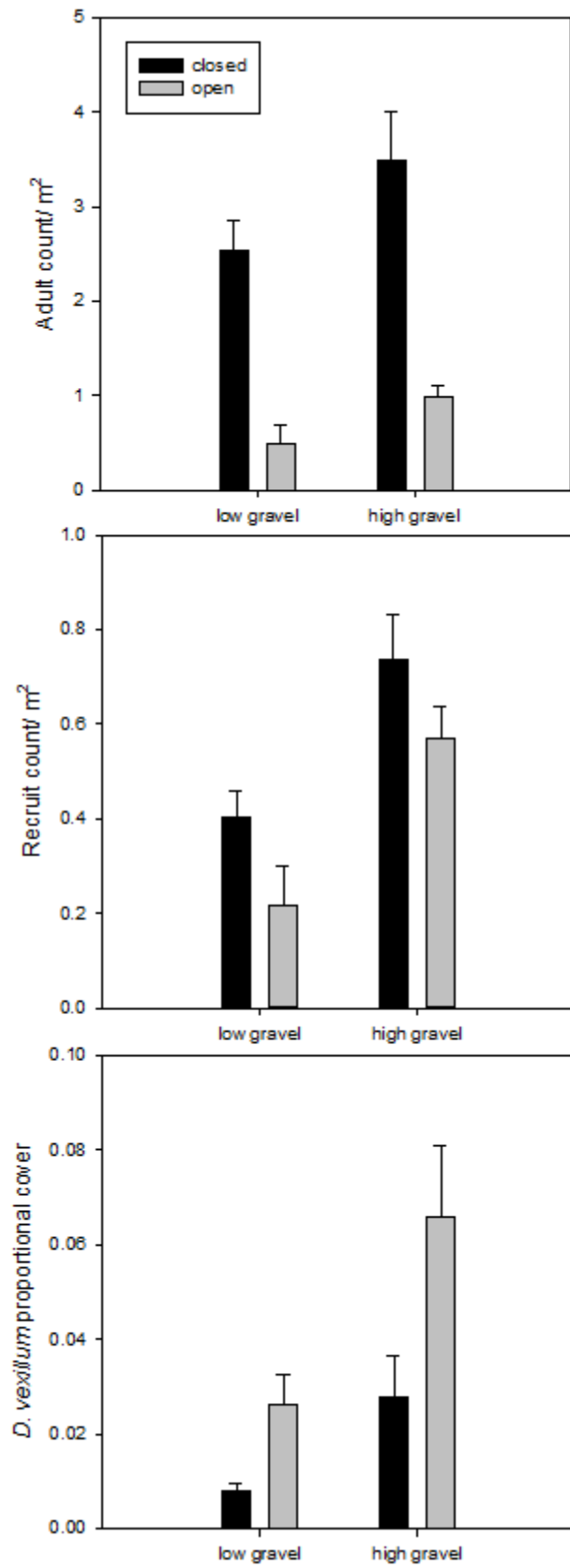


Figure 2.5. (a) Density of adult sea scallops in areas closed and open to bottom-fishing ( $p < 0.001$ ) with gravel substrate ( $p < 0.001$ ) (b) Density of recruit sea scallops in areas closed and open to bottom-fishing ( $p > 0.05$ ) with gravel substrate ( $p < 0.001$ ) (c) Proportional cover of *D. vexillum* in areas closed and open to bottom-fishing ( $p < 0.001$ ) with gravel substrate ( $p < 0.001$ ). The “high gravel” category represents images with greater than or equal to 50% gravel cover, whereas the “low gravel” category is less than 50% gravel. Error bars represent 95% confidence intervals.

### **3.3 Interpolated estimates of *D. vexillum* distribution over the study area**

The kriged estimates of gravel in the study area indicate that 39.8% of the study area is gravel habitat (S1 Appendix a). Universal kriging of *D. vexillum* using the gravel, depth and the categorical predictor region (inside or outside the closed area) as co-variables was conducted to demonstrate the proportion of the study area covered (Figure 2.6).

Interpolated values are as high as 51.7% of area covered with *D. vexillum* in some cells of the prediction grid, with a mean value of the total study area covered being 2.9% (Figure 2.6). The variance of the interpolated proportional cover is also demonstrated showing areas with lower data coverage have higher variance (Figure 2.6). *Didemnum vexillum* is shown to cover significant portions of the study area, with the greatest density shown in the region open to fishing adjacent to Closed Area II.



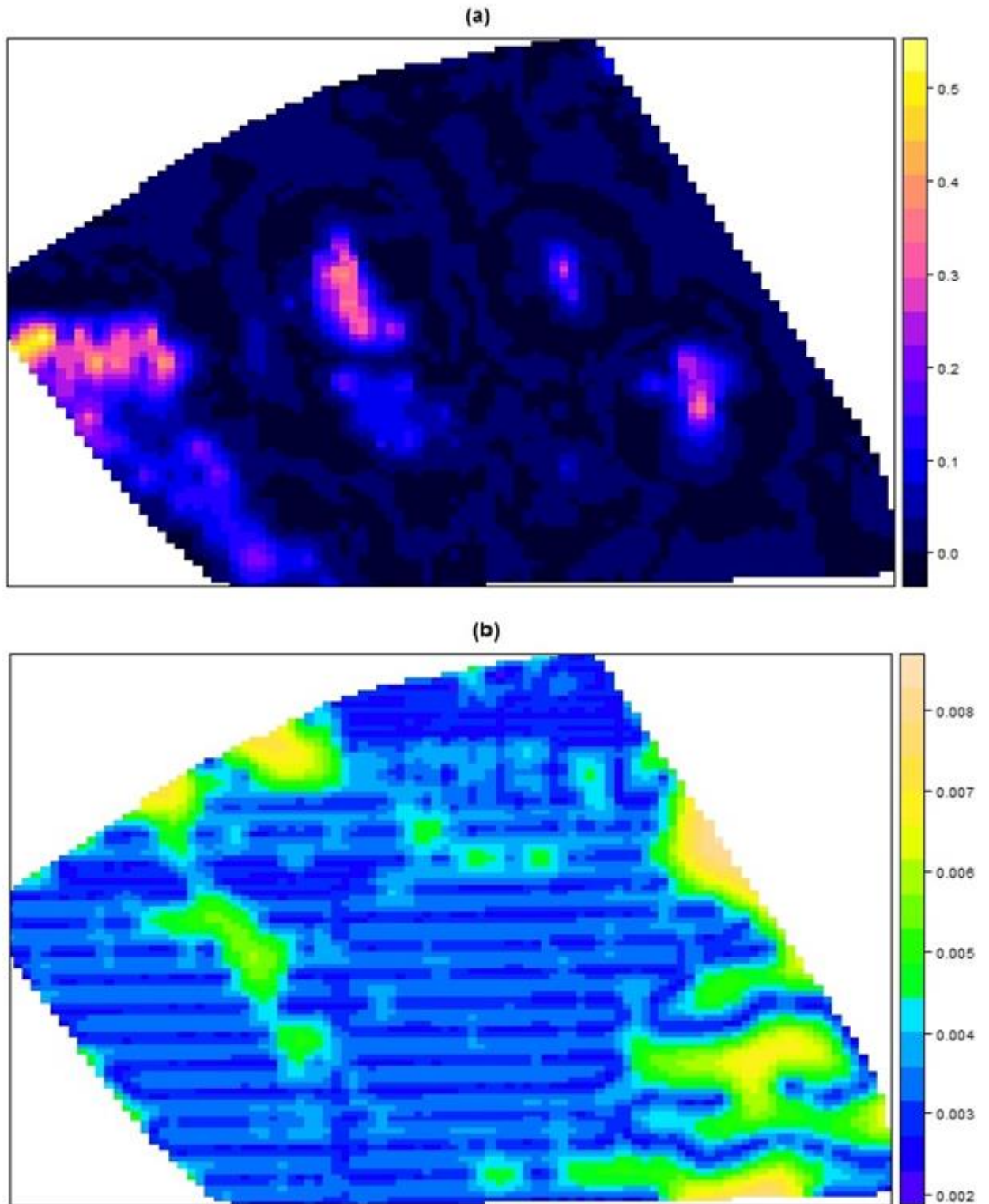


Figure 2.6. (a) *D.vexillum* proportional cover from universal kriging estimates. (b) Variance from universal kriging estimates.

#### 4. DISCUSSION:

##### 4.1 The effect of the invasive *D. vexillum* on sea scallop habitat

The results from this study demonstrate the negative relationship of the invasive *D. vexillum* on sea scallop distributions. We found *D. vexillum* cover is negatively related to adult and juvenile sea scallop densities in both areas that were open and closed to bottom-fishing, and densities of *D. vexillum* were much greater in the region open to fishing, even after controlling for substrate. Additionally, scallops as well as *D. vexillum* appear in greater densities in areas of high gravel substrate, suggesting there is competition for habitat. Our interpolated estimates of gravel proportional cover indicate that 39.8% of the study area is gravel substrate, which is preferred habitat for both scallops and *D. vexillum*. Scallop spat cannot settle on *D. vexillum*, likely as a result of its acidic tunic (Morris et al. 2009). In addition to overgrowing the gravel, ascidian colonies also can cement grains together making it more difficult for scallops to burrow into the substrate (Mercer et al. 2009). Therefore, colonization of gravel substrate by *D. vexillum* turns preferred sea scallop substrate into unsuitable habitat. It is unlikely that *D. vexillum* is outcompeted by scallops in the closed area because *D. vexillum* has been observed to smother scallops and other bivalves by using their shells as substrate (Bullard et al. 2007; Carman et al. 2009). The interpolated estimates of *D. vexillum* demonstrate that it covers significant portions of the study area. In some areas over 50% of the habitat is covered by *D. vexillum* with the mean of the total study area being around 2.9%. In regions open to fishing the mean proportional cover of *D. vexillum* was over 6%, indicating the spread of this invasive species has the potential to cause a loss of fishing grounds and yield for New England fisheries, though more data is necessary to determine

the effects of *D. vexillum* on fishery productivity.

Bottom-fishing methods can cause fragmentation, and therefore may spread *D. vexillum* colonies (Bullard et al. 2007; Morris & Carman 2012). Fragments of *D. vexillum* colonies can lodge in fishing gear and spread to other areas (Daley & Scavia 2008). Additionally sea scallops are typically shucked at sea; discarded scallop shells colonized by *D. vexillum* could potentially generate new colonies (Daley & Scavia 2008). There may also be a possibility that bottom disturbance caused by fishing gear facilitates the spread of *D. vexillum* by clearing the substrate of established native epifauna (Collie et al. 1998; Hermsen et al. 2003). Additionally, the disturbance created from bottom-fishing can also generate more organic matter in the benthos, which could be a significant food source for filter-feeding *D. vexillum* colonies. These mechanisms may explain the relatively lower proportion of *D. vexillum* observed in areas closed to bottom-fishing as found in this study. Alternatively, other factors may also account for the observed differences in *D. vexillum* abundances such as oceanographic conditions, or the initial location where *D. vexillum* was introduced on Georges Bank, which was most likely in the open area via hull-fouling of vessels or commercial fishing. Even if bottom-fishing gear is a primary vector for the spread *D. vexillum*, it can spread by other natural mechanisms, and thus it may eventually occur in greater densities in the closed area.

The time series from the scallop dredge survey (1982-2015) demonstrates a dramatic increase in scallop biomass after the closed areas were put in place in 1994 in both the closed and open areas as a result of management efforts that decreased fishing mortality (Hart & Rago 2006). In particular, the closure of a portion of our study site as part of Closed Area II of Georges Bank induced substantially greater densities of adult

scallops as a result of its protection from bottom-fishing, but at best only a weak, non-significant effect was observed for recruits. The strong closed area effect on adults that are targeted by the scallop fishery is to be expected, but recruits (< 75mm) are much smaller than the 102mm ring size of commercial scallop gear, and thus most recruits would pass through the gear and not be captured. While patterns observed in recruitment from a single year class should be treated with caution, the fact that recruitment was higher in the area closed to fishing, while controlling for substrate, might be due to the lower levels of *D. vexillum* in the protected area. Moreover the spread of *D. vexillum* in our study area coincides with a decline in scallop biomass beginning in 2010, based on the dredge survey data, due in part to reduced recruitment in this area. Thus, the productivity of the scallop fishery may be affected by the inhibiting effects of *D. vexillum* on scallop settlement and recruitment, though further data is necessary to determine the impact on the fishery.

Fish populations may also be affected by the spread of *D. vexillum*. The gravel substrate where *D. vexillum* is found in greatest density also serves as important nursery grounds for juvenile cod and haddock (Collie et al. 2000), as well as spawning grounds for Atlantic herring, so *D. vexillum* may alter habitat and food availability for several commercially important species. Additionally, allelopathic chemicals from *D. vexillum* overgrowing on substrates may negatively impact the viability of eggs of fish that rely on gravel pavement for spawning sites such as Atlantic herring (Dijkstra et al. 2007).

#### **4.2 Management considerations**

In order to manage the spread of *D. vexillum*, further research is necessary to evaluate which of these mechanisms contribute most significantly to spreading this

species. Habitat restoration efforts that include attempts to remove *D. vexillum* from some areas might be considered. Other marine pest species such as jellyfish, ctenophores, nemerteans, snails, sea urchins, polychaetes, burrowing shrimps, crabs, and fishes may be amenable to biological control efforts, though strategies adopted from terrestrial realms require special considerations for marine environments (Lafferty & Kuris 1996; Secord 2003). Sea urchins (*Strongylocentrotus droebachiensis* and *Strongylocentrotus franciscanus*) are predators of *D. vexillum*, though in experimental tests these urchins preferred other food sources when available (Epelbaum et al. 2009). The periwinkle (*Littorina littorea*), which is also not indigenous, is a predator of *D. vexillum*, but it is of limited value since it only consumes senescing *D. vexillum* and is an intertidal to shallow subtidal snail (Valentine et al. 2007a; Carman et al. 2009). Predators were not successful at controlling fouling from *D. vexillum* on Pacific oysters in experimental treatments (Switzer et al. 2011). Thus options for biological control of *D. vexillum* are limited.

Manual eradication methods have been used by shellfish aquaculturists since *D. vexillum* is a shellfish pest capable of encapsulating and smothering bivalves (Carman et al. 2009). For example, chemical and mechanical treatments have been shown to reduce fouling from *D. vexillum* in oyster aquaculture, though survival of oysters was also reduced in lime-treated oysters (Switzer et al. 2011). Eradication methods such as smothering with dredge material, filter fabric, and plastic, as well as manual removal and treating boat hulls with dilute bleach have been used in Shakespeare Bay, New Zealand (Coutts & Forrest 2007). Smothering by dredge material killed 100% of colonies occupying an approximately 3200 m<sup>2</sup> area of relatively homogenous seabed substrate, although efforts were not successful in completely eradicating *D. vexillum* from the

region. However these methods can also have negative effects on native species, thus eradication methods must be used with caution. Additionally, while these methods may be useful for control in small-scale near shore environments, they would be more difficult and expensive to attempt on Georges Bank and may not have lasting benefits (Coutts & Forrest 2007).

As with many marine invasive species, limiting the spread of *D. vexillum* will require controlling transport vectors that facilitate its spread such as vessel fouling, aquaculture, and commercial fishing (Tamburri et al. 2002; Bax et al. 2003; Daley & Scavia 2008). *D. vexillum* most likely spreads through fouling of vessel hulls, aquaculture transfers and commercial fishing (Herborg et al. 2009; Acosta & Forrest 2009). Maintaining databases on transport vectors such as ship movement will provide information that can be used to develop risk assessment programs to control the transport vectors for *D. vexillum* and other nonindigenous species (Daley & Scavia 2008; Herborg et al. 2009; Acosta & Forrest 2009). Additionally environmental niche models combined with vector models can provide spatially explicit predictions of the potential distributions of the invasion to inform risk assessments (Herborg et al. 2009). This information can be used for regulatory agencies to control transport vectors through voluntary or mandatory practices that minimize the risk of spreading *D. vexillum*. Given the value of the sea scallop fishery, controlling the spread of this invasive species has both economic and ecological importance.

## **5. Conclusions**

In this study, we demonstrate a negative relationship between sea scallops and the invasive species *D. vexillum* on commercially important fishing grounds. We also

demonstrated that there are higher concentrations of *D. vexillum* in areas open to bottom-fishing than areas closed to bottom-fishing. Future studies should evaluate the relationship between fishing effort and the spread of this invasive species, to determine the degree to which bottom-fishing is propagating the spread of this invasive and the potential for protected areas to mitigate habitat degradation caused by *D. vexillum*. Management of this invasive species may require coordinated efforts to restore degraded habitat and limit its spread through the various transport vectors discussed. Future studies also may address more long-term monitoring efforts of this invasive species to determine its impact on commercially valued fish species.

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## CHAPTER 3

### INVASIVE TUNICATE RESTRUCTURES INVERTEBRATE COMMUNITY ON FISHING GROUNDS AND A LARGE PROTECTED AREA ON GEORGES BANK

#### **Abstract:**

Marine invasive species can profoundly alter ecosystem processes by displacing native species and changing community structures. The invasive tunicate *Didemnum vexillum* was first found on the northern edge Georges Bank in 1998. It can form encrusting colonies on gravel substrates that are also a preferred habitat for several species of the invertebrate community. In this study we used data collected via HabCam, a vessel-towed underwater imaging system, to investigate the distribution of *D. vexillum* and the relationship of this species to other invertebrates in the benthic community in a portion of Georges Bank that includes fishing grounds and an area protected from bottom-fishing. This novel technology provides high resolution imaging of species distributions in areas of the benthic environment that were previously unobservable. We found that *D. vexillum* density negatively correlates with the density of several species of the invertebrate community. However, it positively associates with densities of crabs of the *Cancer* genus, the tube forming polychaete *Filograna implexa* and sea stars of the genus *Asterias*. The hypothesis that *D. vexillum* restructures the invertebrate community is supported by principal components analysis revealing it as a primary driver of variation in the community when present. Additionally, as consistent with previous studies, there is an effect of the closed area as compared to fishing grounds on the structure of the invertebrate community and the abundance of certain species. Principal components analysis revealed that bottom-fishing also appears to weaken clustering among species in the invertebrate community as compared to the community

structure in the closed area. Biodiversity in high gravel sites, as measured by the Shannon diversity index, also declined with increasing *D.vexillum* percent cover, while the open and closed areas were not significantly different in their level of biodiversity. *Didemnum vexillum* appears to be the key driver of biodiversity decline when present, rather than other processes such as direct disturbance from dredging. This research evaluates ecological responses to the presence of an invasive tunicate and suggests that this invasive species is a major force in shaping the ecological interactions in invaded areas.

## 1. INTRODUCTION:

Marine invasive species are a threat to marine biodiversity and a major contributor of environmental change (Bax et al. 2003, Molnar et al. 2008). Invasive species in marine environments have been shown to displace native species, change community structure and food webs, and alter fundamental ecosystem processes (Molnar et al. 2008). Additionally, marine invasive species can decrease economic activity such as productivity from resources including fisheries, aquaculture and tourism (Lovell & Stone 2005, Williams & Grosholz 2008, Molnar et al. 2008, Vilà et al. 2010). The primary vectors for the introduction of marine invasive species are ship fouling, ballast water, and accidental introductions from mariculture, fisheries and the aquarium trade (Grosholz 2002, Bax et al. 2003, Padilla & Williams 2004, Herborg et al. 2009). Marine coastal environments are the most heavily invaded ecosystems (Ruiz et al. 1997, Molnar et al. 2008, Reusch et al. 2010). It is nearly impossible to eliminate marine invasive species once they become established in marine ecosystems, therefore management efforts are most likely only effective in reducing their impacts (Carlton & Ruiz 2005). Furthermore, there is a paucity of information on marine invasive species and data are often found to be not comparable (Ricciardi et al. 2000, Thresher & Kuris 2004, Crall et al. 2006), which highlights the need for



additional research aimed at understanding invasive species impacts on marine ecosystems.

Invaded communities that are distinct from the native environment of the invasive species may afford an ecological advantage for invasive species due to a lack of shared evolutionary history with species in the invaded community (Keane & Crawley 2002, Mitchell & Power 2003). For example, the enemy-release hypothesis states that the introduced species have left the community that was shared with co-evolved natural enemies and consequently the lack of natural predators makes them safer than other prey species in the invaded community (Colautti et al. 2004, Liu & Stiling 2006). Furthermore, the competitive release hypothesis indicates that release from competition in habitats with new competitors or no competitors allows invasive species to thrive (Blossey & Notzold 1995). Additionally, novel prey may be well-defended against introduced predators than co-evolved predators (Strauss et al. 2006, Salo et al. 2007). Any of these mechanisms can cause introduced species to have wide spread community impacts.

Alternatively, the biotic resistance hypothesis proposes that introduced species may be limited by native enemies that they have not developed defenses or competitive advantages against (Colautti et al. 2004, Levine et al. 2004). Determinants of establishment success are specific to species and location in marine ecosystems (Stachowicz et al. 1999, Nyberg & Wallentinus 2005). For example, species with high dispersal capabilities, a range of climatic tolerances and competitive abilities are generally successful invaders (Nyberg & Wallentinus 2005). Locations in the marine environment that permit the introduction of species harbor less diverse communities (Stachowicz et al. 1999). The insurance hypothesis, similar to the biotic resistance hypothesis, states that species diversity enables some native species to use the majority of the resources available leading to decreased opportunities for non-indigenous species (Yachi & Loreau 1999). In fact, increased species richness has been shown experimentally to enable

biotic resistance to marine invasive species (Stachowicz et al. 1999, Marraffini & Geller 2015). Areas low in diversity and abundance may facilitate invasions and these patches, once colonized by invasive species, may resist both native and non-native species recruitment (Marraffini & Geller 2015). Additionally, invaders may take advantage of other drivers of habitat modification interacting synergistically to alter habitats and limit native species (Gurevitch & Padilla 2004, Didham et al. 2005, 2007a). Generally, habitats that are disturbed have been found to be more susceptible to invasive species (Lozon & MacIsaac 1997, Marvier et al. 2004).

It has been difficult for researchers to disentangle the effects of habitat modification and invasive species on native species diversity leading to debate about the direct and indirect processes driving invasive species dominance (MacDougall & Turkington 2005, Didham et al. 2005, Chabrierie et al. 2008). Habitats with invasive species are generally modified by other processes, therefore it is frequently unclear if the invasive species drive native species loss and declines in biodiversity, if they are opportunists taking advantage of habitat modified by other processes in which low diversity enables their dominance, or if disturbance causes both ecological change and invasion independently (MacDougall & Turkington 2005, Didham et al. 2005, Chabrierie et al. 2008). While the driver hypothesis states that invasive species drive ecosystem changes, the passenger hypothesis posits that other processes drive ecological change and invasive species then are able to dominate environments as an indirect consequence (MacDougall & Turkington 2005). While some studies have supported the passenger hypothesis (MacDougall & Turkington 2005, Chabrierie et al. 2008, Grarock et al. 2014, South & Thomsen 2016), other studies have found that invasive species are the drivers of ecological change (Hermoso et al. 2011, White et al. 2013). Another alternative hypothesis is the ‘back-seat driver’ hypothesis which states that the invasive species requires and benefits from disturbance to

ecosystem processes leading to the decline of native species, but then the invasive contributes to further declines of native species (Bauer 2012), which other studies have also supported (Berman et al. 2013, Fenesi et al. 2015). Although disentangling these forces is difficult, large scale in situ observations of invasive species in habitats characterized by different disturbance regimes can help elucidate the forces driving community change.

In 1998, an invasive sea squirt *Didemnum vexillum* was detected on Georges Bank (Bullard et al. 2007a). *Didemnum vexillum* originated from coastal Japan (Stefaniak et al. 2012) and is a global invader that has spread to Europe, New Zealand and both coasts of North America (Kott 2002, Bullard et al. 2007b, Gittenberger 2007). Additionally, *D.vexillum* has colonized at least 230 km<sup>2</sup> of pebble-gravel habitat on Georges Bank (Valentine et al. 2007). This tunicate is considered a nuisance species because it can foul ship hulls and maritime structures in addition to invading shellfish aquaculture sites and fishing grounds (Daley & Scavia 2008, Carman et al. 2009). *Didemnum vexillum* can reproduce both sexually and asexually, however asexual reproduction and fragmentation are most likely the method by which the species spreads (Lengyel, et al. 2009). Although, the species is a widespread invader it has limited natural dispersal since larvae only remain in the water column for generally less than one day (Osman & Whitlatch 2007). Additionally, there is limited information on the ability of this species to spread naturally via floating debris or other means. However, anthropogenic transport is considered the primary vector for the spread of this species long-distance (Osman & Whitlatch 2007, Herborg et al. 2009). The most probable transport vector for *D.vexillum* is direct transport of colonies fouled on aquaculture equipment, boat hulls or other mobile structures, or the indirect transport of colony fragments where small parts of the colonies break off during transport or disturbance by dredging or trawling (Herborg et al. 2009).

Additionally, *D. vexillum* has been shown to invade habitat of a highly valued commercial shellfish fishery on Georges Bank (Kaplan et al. in review). The characteristics of *D. vexillum* have resulted in rapid population growth such as, early maturation, rapid colony growth due to asexual budding and spread via colony fragmentation, ease of attachment to firm substrates, toleration of a wide range of temperatures, and the lack of natural predators (Bullard et al. 2007, Carman et al. 2009, Valentine et al. 2009). The combination of these characteristics leads *D. vexillum* to outcompete other benthic epifaunal and macrofaunal species. For example, *D. vexillum* has been shown to inhibit other benthic species from settling and growing on colony surfaces due to acidic and organic allelopathic compounds in their tunics (Valentine et al. 2007, Carman et al. 2009, Morris & Carman 2012).

The presence of closed areas on Georges Bank provides a unique opportunity as a location for collecting control data to compare to a habitat disturbed by dredging on benthic community structure. The habitat camera mapping system (HabCam), a vessel-towed underwater camera system, was recently deployed in the Georges Bank and Mid-Atlantic regions. HabCam image data can provide a wealth of information on the habitat of commercial species, non-target species and invasive species as well as information on the impacts of fishing gear used in this region. These data provide visual surveys of invertebrate communities in their habitat without disturbing the habitat itself. The HabCam system can be used to address questions related to the extent of damage bottom-fishing incurs in benthic marine habitats and the extent of invasion from an introduced species. Several studies indicate that dredging disturbances reduce the diversity and abundance of benthic communities in the region (Auster et al. 1996, Collie 1997). Further studies indicate that bottom-fishing gear damages epifaunal taxa, thereby reducing habitat complexity (Jennings & Kaiser 1998, Fogarty & Murawski 1998).

However, no studies in this region have examined the interaction of disturbance from dredging with the spread of an invasive species. Data from the HabCam system can be used to address questions about the relative importance of disturbance from bottom-fishing and invasive species on biodiversity. Evaluating the ecosystem level effects of these processes will provide valuable information to managers seeking to fully assess the extent of management actions beyond the target species.

In this study we use data collected from the habitat camera mapping system (HabCam) to explore the spatial distribution of benthic marine invertebrates and *D. vexillum* in areas protected and unprotected from bottom-fishing on Georges Bank. We hypothesized that the presence of *D. vexillum* alters the benthic community and is the primary driver of biodiversity decline. We assessed how the invertebrate community changes in the presence of *D. vexillum* using principal components analysis and we evaluated correlations between invertebrate species density and *D. vexillum* density. We also determined if bottom-fishing influences associations among species using principal components analysis and assessed if the abundances of these invertebrates is greater in areas open or closed to bottom-fishing. Using the closed area as a control to compare to the area disturbed by bottom-fishing, we evaluated if *D. vexillum* or disturbance from bottom-fishing is the main driver of biodiversity loss. This work can further our understanding of invasive species as a direct or indirect influence on biodiversity and ecological communities. The closed area, where bottom-fishing is prohibited, and the open area disturbed by bottom-fishing provide a natural experiment for assessing the impact of an invasive species relative to dredging disturbance on biodiversity and invertebrate communities.

## 2. METHODS:

### **Study area**

Georges Bank is a shallow, highly productive, submerged plateau off the coast of New England that supports several valuable commercial fisheries (Butman & Beardsley 1987). Surficial sediments of Georges Bank are dominated by large expanses of sand substrate interspersed with gravel and gravel/sand regions that mainly occur on its northern and western portions (Twichell et al. 1987). On the northeastern part of the bank, currents transport sand into deep water leaving gravel habitat along the northern edge. The study site is located in the northeastern portion of Georges Bank, in the area bounded between 41° 49' N and the northern edge of the bank, the Hague line dividing the U.S. and Canadian E.E.Z. on the east, and a boundary parallel to the Hague line on the west (Figure 3.1). The portion to the west of 67° 20' is open to fishing, while the portion to the east has been closed to all groundfish and scallop gear since December 1994, and is a part of Closed Area II. This area contains both sand and gravel substrates as well as high densities of *D. vexillum* in some locations (Figure 3.2).

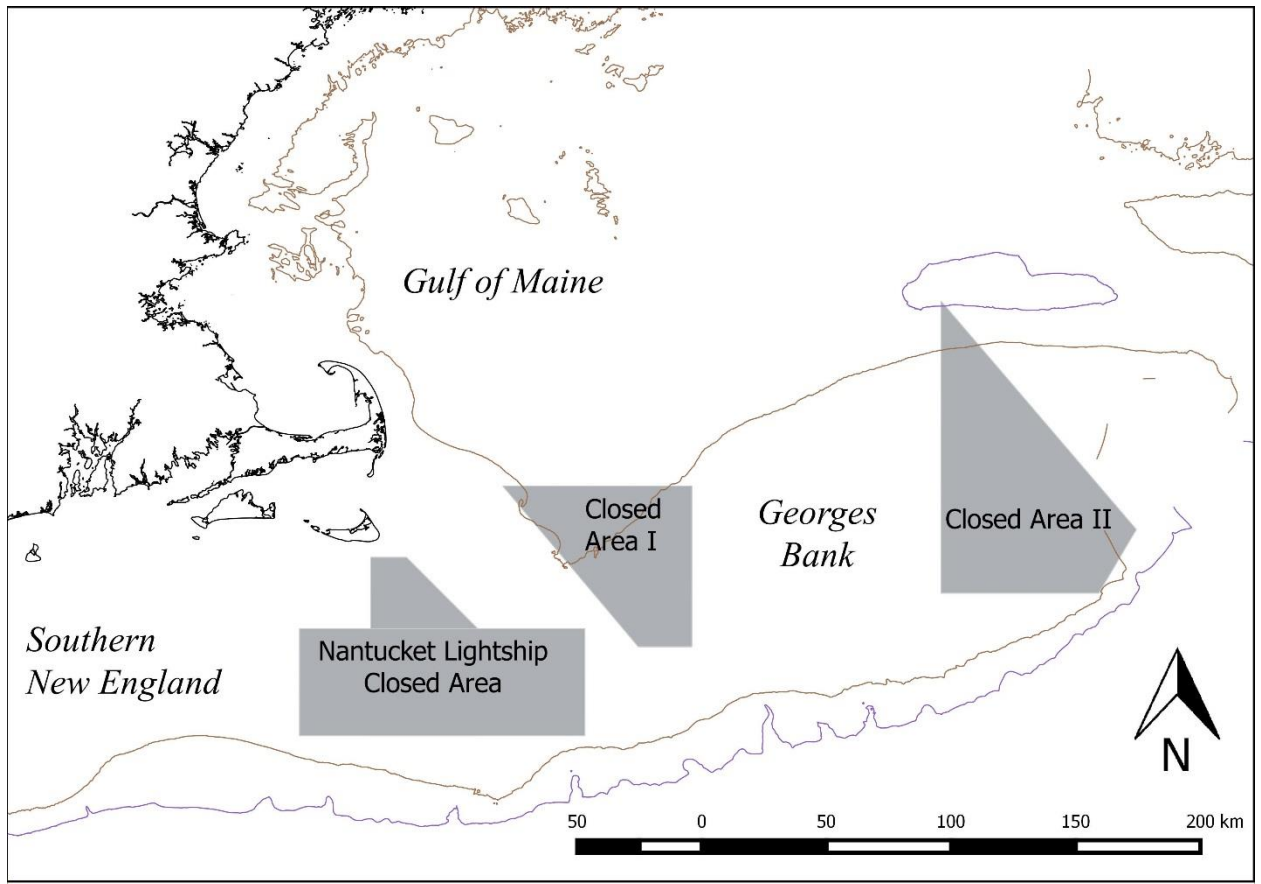


Figure 3.1. Georges Bank, with closed areas.

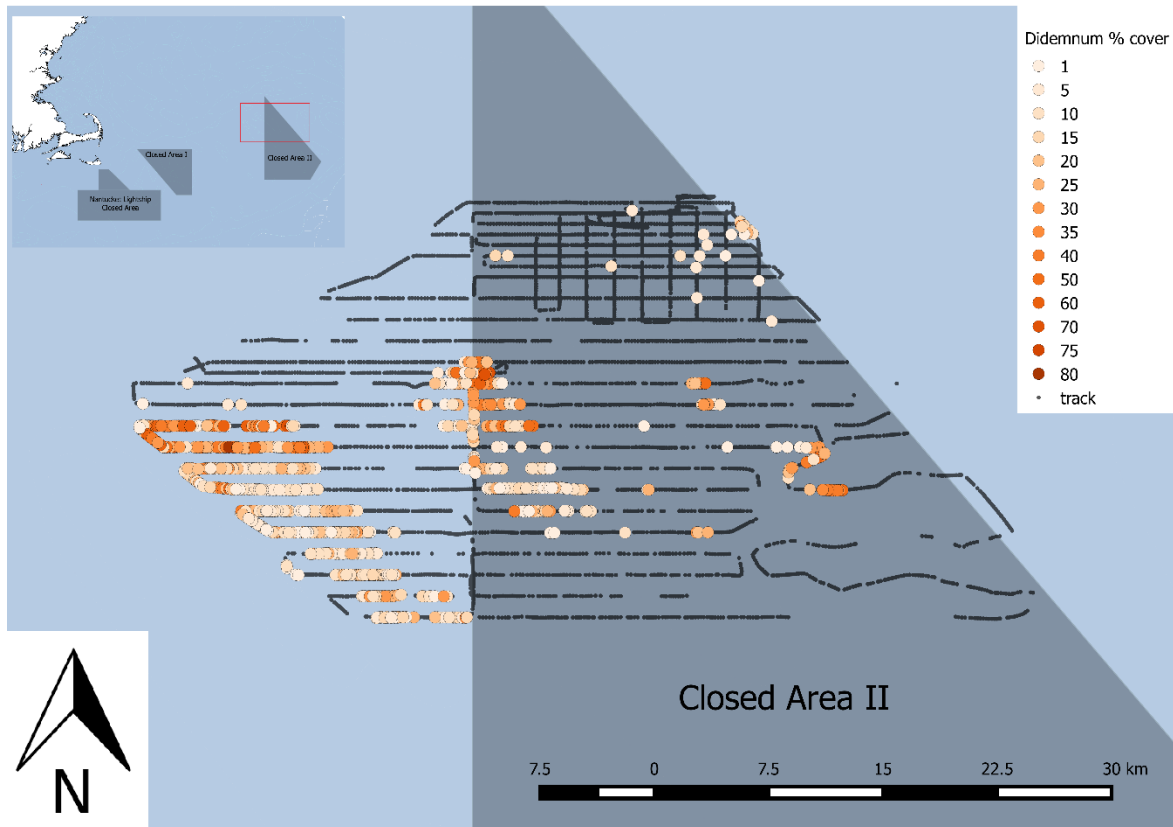


Figure 3.2. Map of Closed Area II with HabCam track showing percent *Didemnum vexillum* cover from 2012 survey.

### Data collection

Data for this project was collected from HabCam (v2), a high resolution imaging system that provides visual surveys of benthic marine organisms without disturbing the habitat itself (Howland et al. 2006, Taylor et al. 2008, York et al. 2008). These data can be used to evaluate physical features of the environment that drive spatial and temporal variability of benthic invertebrates. The HabCam vehicle is towed at speeds of 5-6 knots during which it collects data at a rate of about six images per second providing a continuous band of data input along the survey track. The equipment on HabCam v2 includes a digital still camera (UNIQ Vision, Inc. UP-1800-CL), four machine vision strobes (Perkin Elmer MVS-5000) mounted in underwater housings placed radially around the camera 50 cm apart. Other sensors on HabCam v2 include a



CTD (SBE 37-IS MicroCat, Seabird electronics Inc.) for conductivity and temperature measurements, a YSI 6600 Sonde multiparameter sensor, and a Benthos altimeter (PSA-916), which measures distance from the vehicle to the bottom. The data for this project was collected on the F/V Kathy Marie by HabCam v2 in July of 2012 in and to the west of the northern portion of Closed Area II (Figure 3.2).

### **Data processing:**

HabCam images were annotated to identify members of the invertebrate community, which were identified to species, genus or family level depending on the species for one in every 200 images collected by HabCam v2 during the July 2012 survey (K.H.). In total 5,309 images were annotated for members of the invertebrate community both in and adjacent to Closed Area II (Figure 3.2).

Locations of invertebrates were identified as being inside or outside of the closed area using the intersect and difference geoprocessing tools in Quantum GIS (QGIS development team 2015) and these were subsequently separated for analyses. Density estimates for each species were obtained by dividing species counts by the area of the field of view for each image. Sediment composition was evaluated visually based on the fraction of the image covered. Bryozoan and *D. vexillum* percent cover was also evaluated based on visual estimates of the fraction of the image that it covers.

### **Data analysis**

#### *Species interactions with D.vexillum*

Interactions with *D.vexillum* were assessed in the open and closed areas using hurdle models where the presence or absence of the species was modeled using a generalized linear model under a binomial distribution, then the nonzero count data were modeled using a Poisson

distribution to identify the relationship between the density of each species using *D.vexillum* as a predictor (Potts & Elith 2006). The coefficients from presence-absence and count model predictions were then multiplied to create the final predictions used in the analysis shown (Figure 3.3). Hurdle models were used since there were a large number of images containing zero species. Over-dispersion was detected for many species; therefore for these species a Poisson quasi-likelihood was used to fit the GLMs, in which the variance is given by  $\Phi * \mu$ , where  $\mu$  is the mean density and  $\Phi$  is the overdispersion parameter, thus allowing the variance to be greater than the mean. Additionally, gravel substrate was used as a predictor in all models with gravel held at the mean value for model predictions since substrate also was a main predictor of species distributions. Data for all species and percent gravel cover were first averaged based on approximately 1 km blocks to reduce localized noise as well as spatial auto-correlation. Additionally associations among species were assessed using principal components analysis (PCA) in the presence and absence of *D.vexillum* to assess if *D.vexillum* restructures associations among species. A scaled correlation matrix was used for all principal components analyses since species were assessed on different scales, as counts or percent coverage.

#### *Closed area effect on invertebrate community*

The influence of the protected area on the invertebrate community was analyzed using analysis of covariance (ANCOVA) with the percentage gravel substrate as a covariate, since most of the species analyzed appear to correlate positively with gravel. Co-linearity was observed between the two most dominant substrate types, gravel and sand (adjusted  $R^2=0.875$ ), and hence only gravel was used as a covariate in the analyses. Associations among species were determined using principal components analysis (PCA) in the open and closed areas. Additionally, the Shannon biodiversity index was calculated for the areas open and closed to fishing with all sites

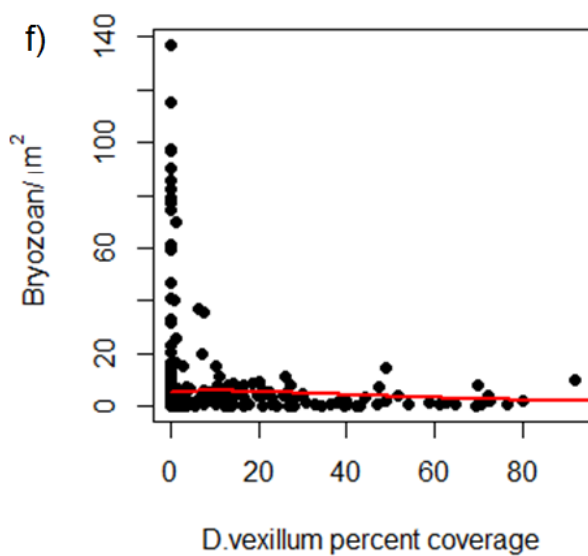
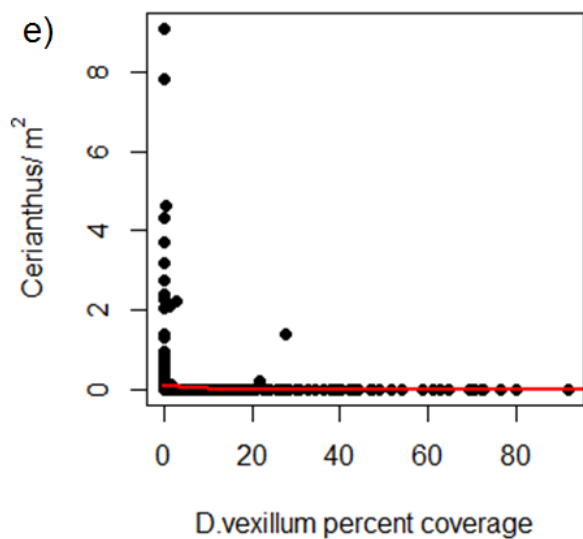
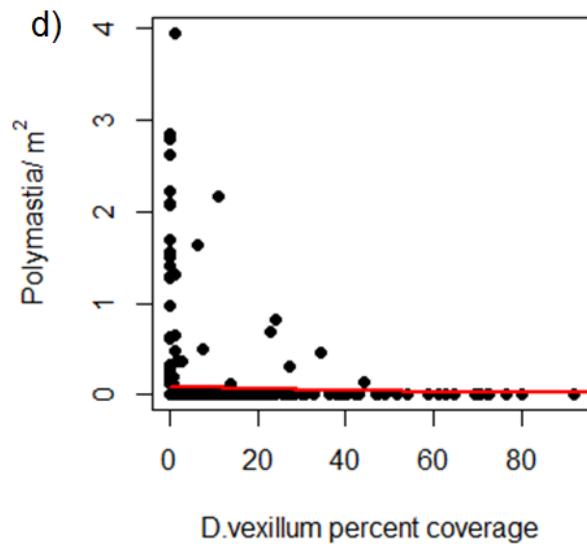
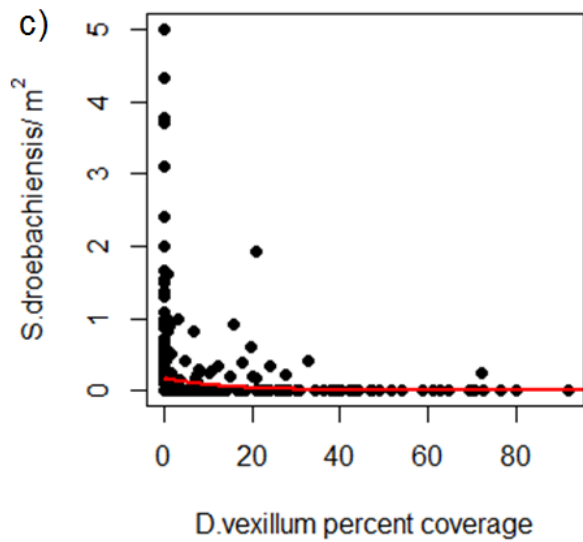
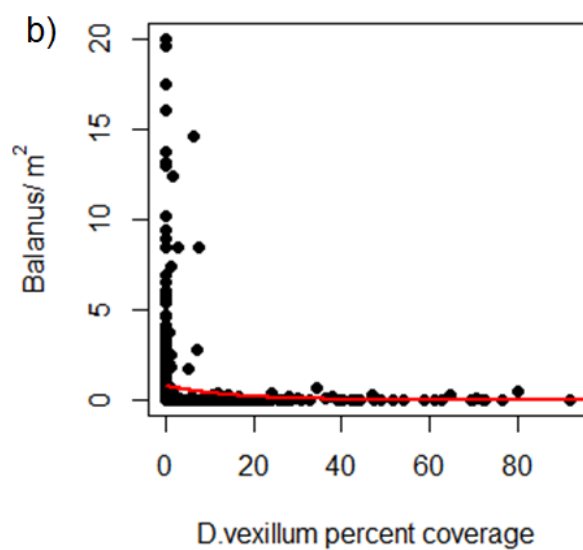
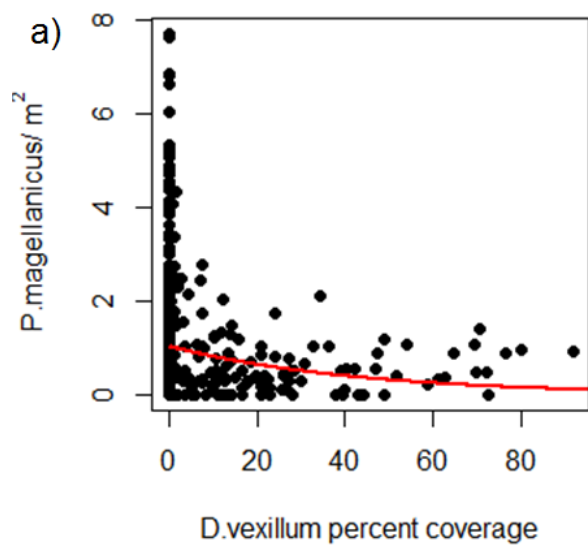
pooled by area to indicate overall which area contained greater biodiversity. The influence of *D.vexillum* and the closed area effect were also assessed by measuring species diversity using the Shannon diversity index calculated per site. Areas containing high gravel (>50%) were separated from non-gravel areas for the site-level biodiversity analyses.

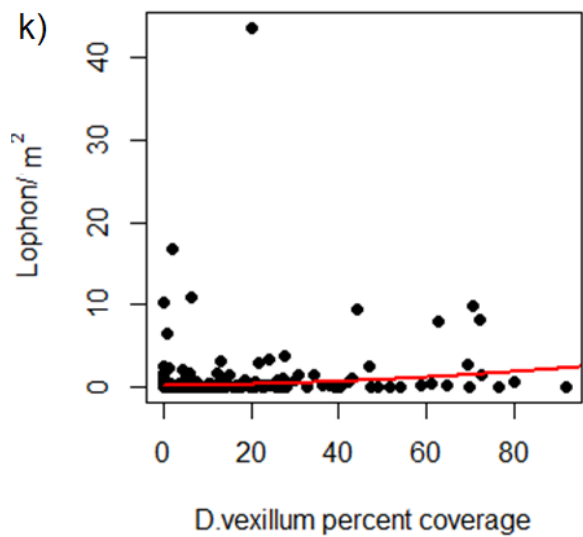
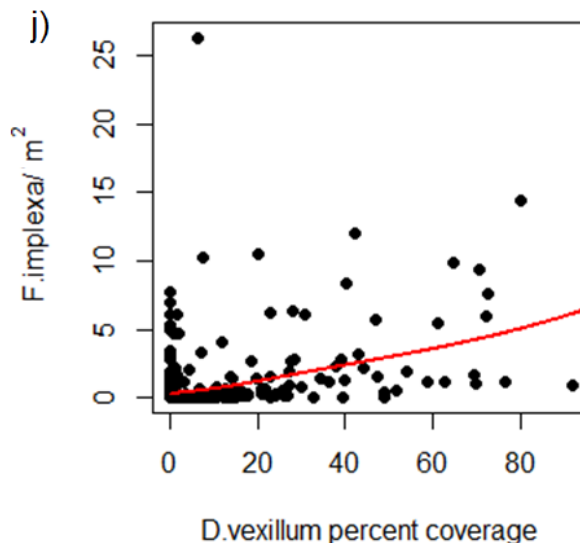
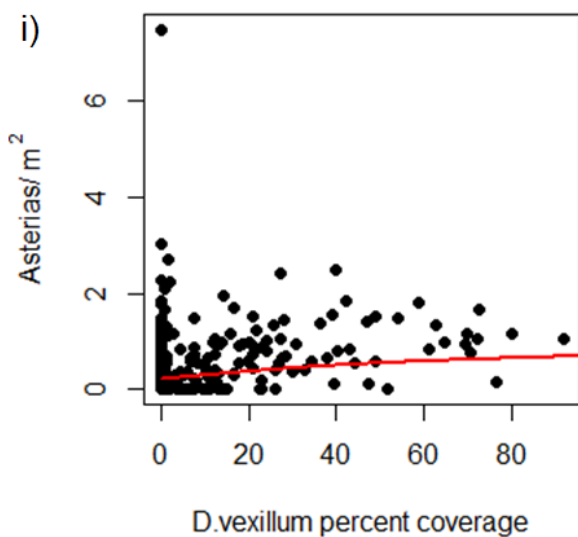
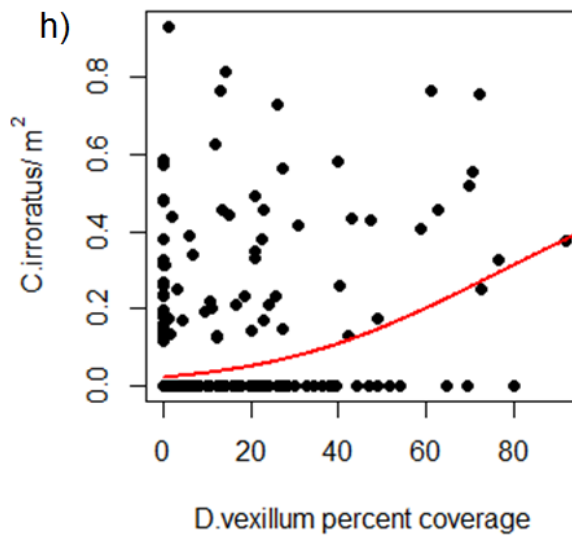
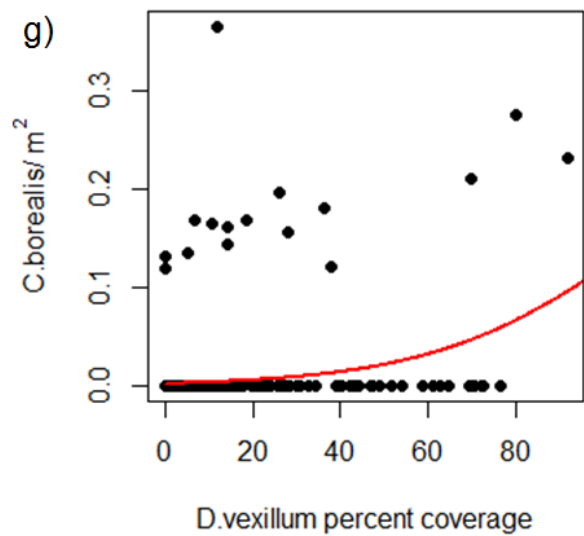
### 3. RESULTS:

#### *Species interactions with D.vexillum*

Based on model fits using the hurdle models, species demonstrating a negative correlation to percent coverage of *D.vexillum* were the Atlantic sea scallop (*P.magellanicus*), barnacles (genus *Balanus*), the tube anemone (genus *Cerianthus*), the green sea urchin (*S.droebachiensis*), the globular sponge of the genus *Polymastia*, and bryozoans (Figure 3.3 a-f). A positive correlation was observed with the *Cancer* crabs (*C.irroratus* and *C.borealis*), sea stars of the genus *Asterias*, sponges of genus *Lophon* and the lacy tubeworm (*Filograna implexa*) (Figure 3.3 g-k). Several species showed no significant correlation with *D.vexillum* in the hurdle models including the sunstar *Crossaster papposus*, mussels of the family *Mytilidae*, marine worms of the genus *Myxicola* and the stalked tunicate (*B.overifera*) (Figure 3.3 l-m). HabCam images are shown of *D.vexillum* with some species which it positively associates with such as *Asterias* sea stars, the *Cancer* crab *C.borealis*, the encrusting sponge of the genus *Lophon* as well as species it negatively associates with such as, sea scallops (*P.magellanicus*) and barnacles (*Balanus*) (Figure 3.4 a-d). Sea stars appear to traverse areas with patchy *D.vexillum* infestation (Figure 3.4 c). However, no other species appear in areas that are almost entirely covered with *D.vexillum* (Figure 3.4 a). In high gravel habitat, principle components analysis (PCA) demonstrated that *D.vexillum* was a strong driver of variation among sites in the first principal component when present in the community in closed and open areas (Figure 3.5). The invertebrate community

without *D.vexillum* appears to be characterized by three distinct associations, whereas groupings among these species are rearranged in the presence of *D.vexillum* (Figure 3.5 a-d). The community of species that exists in the area despite the presence of *D.vexillum* is comprised of species such as the sunstar (*Crossaster papposus*), bryozoans, mussels of the family *Mytilidae*, and the stalked tunicate *B.verifera*, which appear in the PCA as a distinct community orthogonal to the *D.vexillum* community (Figure 3.5 b, d). Also, the marine worm (*Myxicola*), the sunstar *C. papposus* and the Jonah crab (*C.borealis*) were not found in open area sites without *D.vexillum*, showing overall lower species richness. The sunstar *C. papposus* was also not present in closed area sites without *D.vexillum* since these species are relatively rare on Georges Bank. The total number of *C. papposus* sunstars found was 19 out of 5,309 images annotated in this study, while the total number of Jonah crabs *C.borealis* found was 18 indicating these two species are rare in this area in comparison to all other invertebrate species for which over 100 individuals of each species were found, shown in a rank abundance plot (S1 Appendix C).





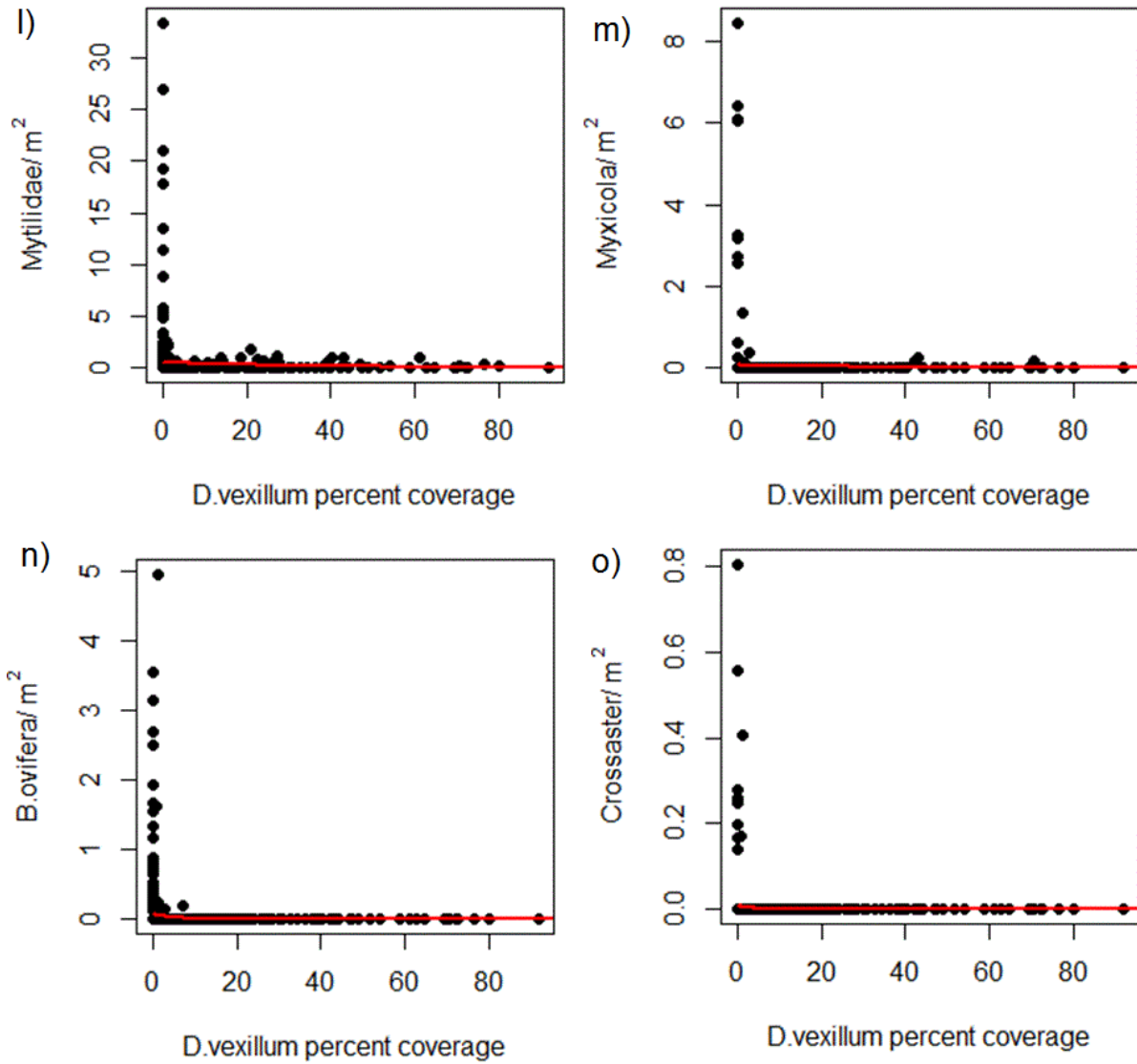


Figure 3.3. Model fits for relationship of *D.vexillum* and other invertebrate species in benthic community using hurdle models.

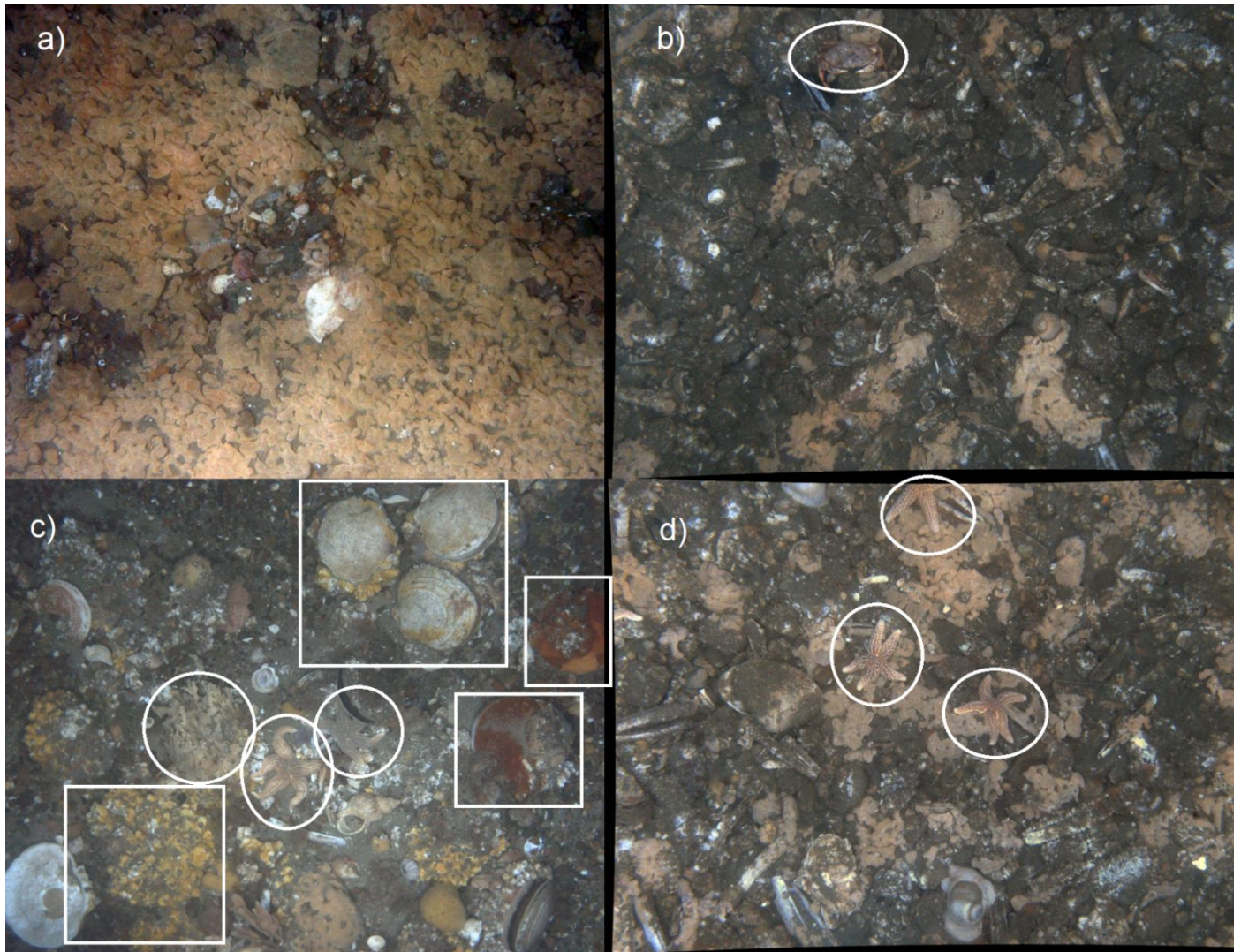


Figure 3.4. Images from Habcam with invertebrate species positively associating with *D.vexillum* shown in circles, species with negative association with *D.vexillum* shown in squares. a) *Didemnum vexillum* covering benthic environment. b) *Cancer* crab with *D.vexillum* patches. c) Sea scallops (*P.magellanicus*), barnacles (*Balanus*), sea stars (*Asterias*), and encrusting sponge of the genus *Lophon*. d) Sea stars (*Asterias*) over *D.vexillum* patches.



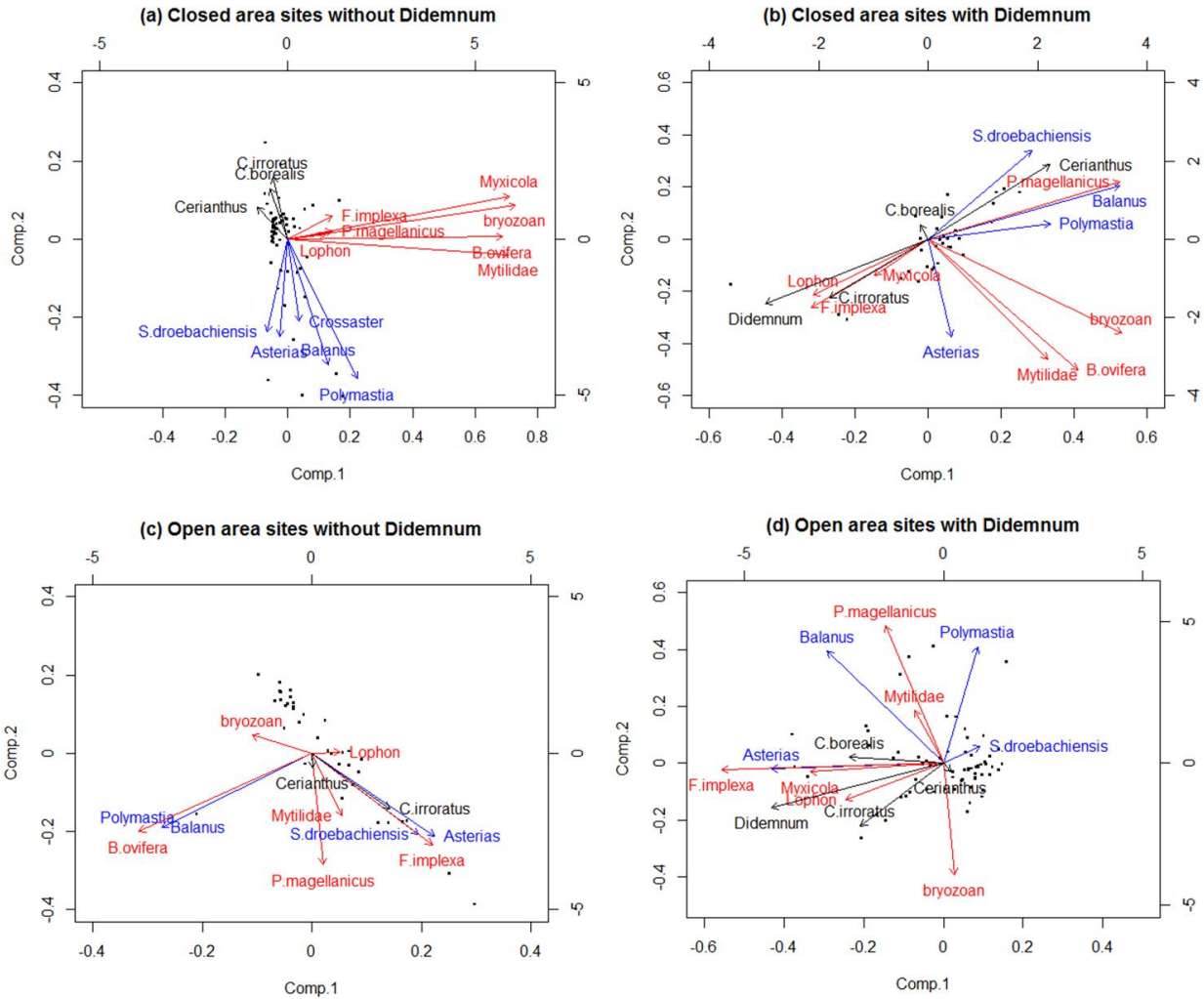


Figure 3.5. Sites with greater than 50% gravel substrate (a) closed areas without *D. vexillum*, (b) closed areas with *D. vexillum* present, (c) open areas without *D. vexillum* and (d) open areas with *D. vexillum* present.

*Closed area effect on invertebrates:*

The effect of the protected area was assessed using ANCOVA with significant interactions shown (Table 3.1, Figure 3.6 a,b). Barnacles of the genus *Balanus*, sea scallops (*P. magellanicus*), the green sea urchin (*S. droebachiensis*), bryozoans, mussels (family *Mytilidae*), the marine worm (genus *Myxicola*), globular sponges (genus *Polymastia*), and the stalked tunicate (*B. ovifera*) were more abundant in the closed area than the open area (Figure

3.6). Conversely, sea stars (genus *Asterias*), the tube anemone (genus *Cerianthus*), the encrusting sponge (genus *Lophon*), the sunstar (*Crossaster papposus*), *D.vexillum*, the lacy tubeworm (*F.implexa*), and the crabs (*C.irroratus* and *C.borealis*) were found in greater abundance in the area open to bottom-fishing (Figure 3.6). Associations among species change in the open area as compared to the closed area indicating bottom-fishing influences these relationships (Figure 3.5 a-d). A distinct group is present with *D.vexillum* in both the open and closed area PCA, though this group is more closely clustered in the area closed to fishing than the area open to fishing. However, *Asterias* sea stars and the crab *C.borealis* associate more closely with the *D.vexillum* community in the area open to bottom-fishing, but are not part of that community in the closed area (Figure 3.4, Figure 3.5).

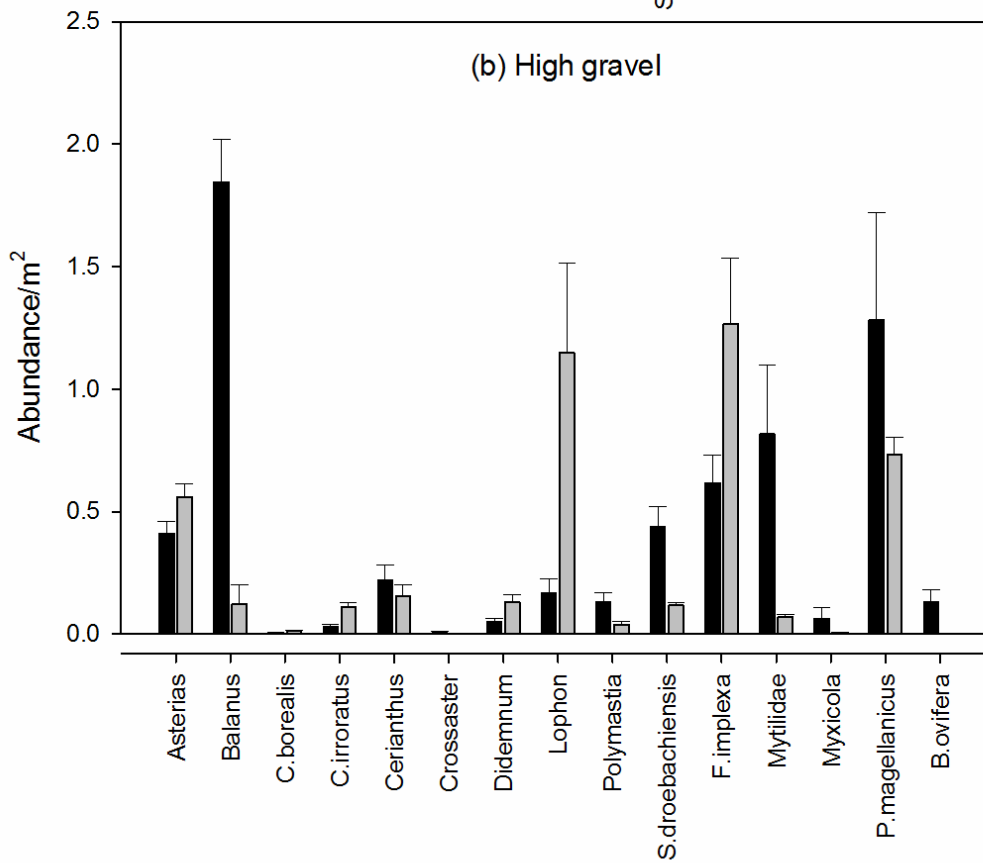
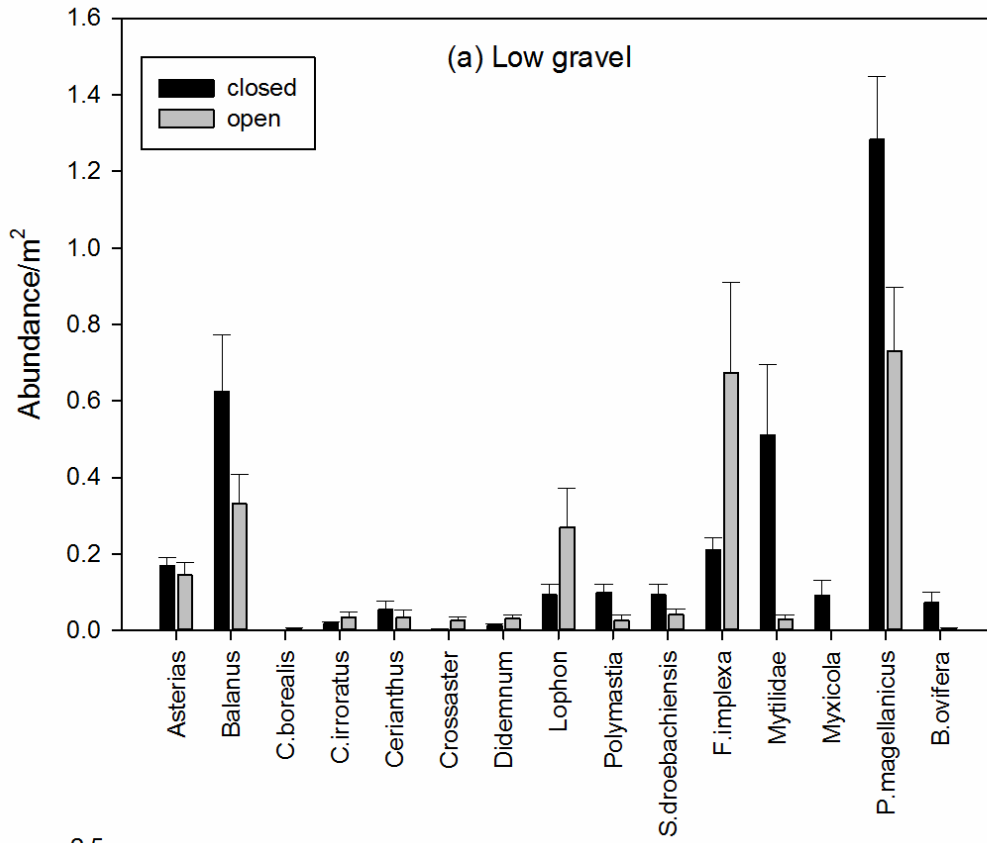


Figure 3.6. The effect of the closed area on abundances of benthic invertebrate species in (a) low gravel and (b) high gravel habitats. ANCOVA results are reported in Table 1.

Table 3.1. Closed area effect on invertebrate species of Georges Bank. Analysis of covariance (ANCOVA). Significance levels: \*p<0.05, \*\*p<0.01, \*\*\* p<0.001

Species	Closed area effect (+/-)	Gravel coefficient	Interaction
<i>Balanus</i>	*** (+)	0.021**	**
<i>P. magellanicus</i>	*** (+)	0.016***	
<i>Asterias</i>	*** (-)	0.009***	
<i>S. droebachiensis</i>	* (+)	0.006***	**
<i>Bryozoan</i>	*** (+)		
<i>Mytilidae</i>	** (+)		
<i>Cerianthus</i>		0.004***	
<i>Mxyicola</i>	* (+)		
<i>Lophon</i>	*** (-)	0.001**	**
<i>Polymastia</i>	* (+)		
<i>Crossaster</i>			
<i>Didemnum</i>	*** (-)	0.13***	**
<i>F. implexa</i>	*** (-)	0.01***	
<i>B. ovifera</i>	** (+)		
<i>C. irroratus</i>	*** (-)	0.0003***	*
<i>C. borealis</i>	** (-)	1.06 x 10 <sup>-4</sup> *	

#### *Didemnum vexillum* and bottom-fishing impacts on biodiversity

The closed area contained greater biodiversity when sites were pooled resulting in a Shannon index of 1.83, compared to the open area with pooled sites having a Shannon index of 1.46. The total abundance of all counted species in the closed area was 4459 individuals, whereas in the open areas the total abundance was 1150 individuals. *Didemnum vexillum* and bryozoans were assessed by percent coverage and not included in count totals.

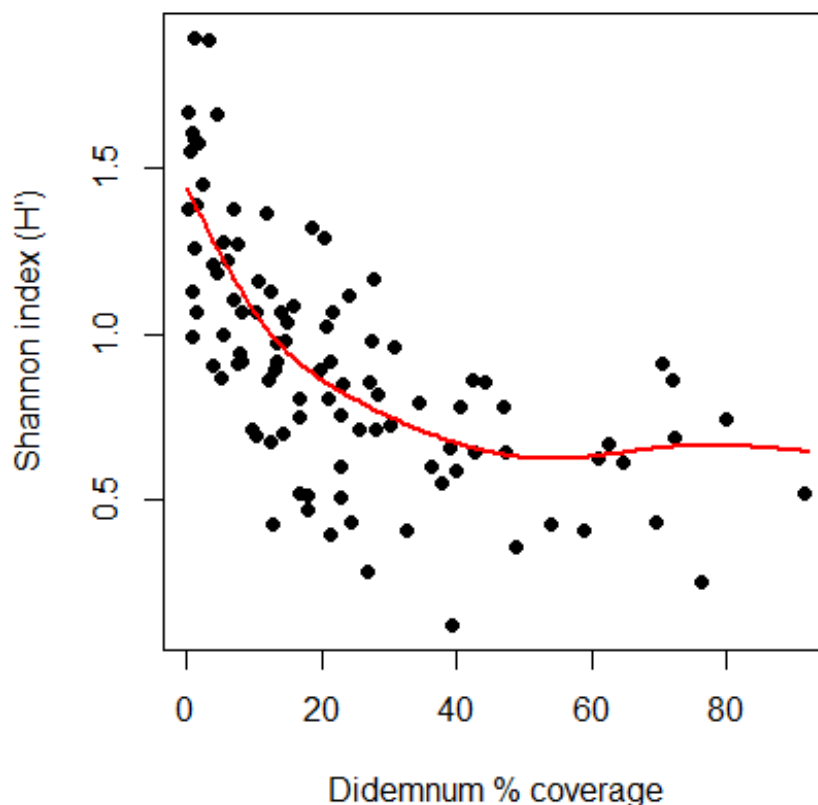


Figure 3.7. *Didemnum vexillum* impacts on biodiversity as measured by Shannon index of biodiversity per site in high gravel habitat only. A generalized additive model was used to predict Shannon index response to *D.vexillum*, gravel percent cover and Area (closed or open) (Table 3.2).

Table 3.2 Generalized additive model fit for Shannon index response to *D.vexillum*, gravel and Area predictors (p<0.001=\*\*\*, p<0.01=\*\*,p<0.05=\*)

Response variable	D. vexillum (edf)	Area (SE)	Gravel (edf)
Shannon index Deviance explained =65%	*** (3.91)	-0.065 (0.05) Not significant	* (6.60)

#### 4. DISCUSSION:

The presence of *D.vexillum* appears to shift associations among species since it is a major driver of variation among sites when present in the community. Increasing percent coverage of *D.vexillum* also demonstrated a decline in biodiversity as measured by the Shannon index, though the effect of the different disturbance regimes, open or closed to bottom-fishing, had no significant effect on the decline in biodiversity observed (Figure 3.7). This finding indicates that *D.vexillum* is the major driver of biodiversity decline particularly when it comes to dominate the community, rather than other causes of habitat modification such as disturbance from bottom-fishing. Additionally, species associated together in the absence of *D.vexillum* appear to aggregate based on a positive or negative association with *D.vexillum*, creating a realignment in the invertebrate community when it is present (Figure 3.5). *Didemnum vexillum* positively associates with some invertebrates, which may have more tolerance to the acidic tissues the tunicate produces, while it appears to have negative associations with other key species of the benthic environment that may be more sensitive to its presence. For example the *Cancer* crabs *C.borealis* and *C. irroratus*, the lacy tubeworm *F.implexa* and sea stars of the *Asterias* genus are positively correlated with *D.vexillum* when modeling each species' response to *D.vexillum* independently. In assessing the multivariate PCA of high gravel habitat, more motile species, such as the *Cancer* crab *C.irroratus*, as well as less motile species such as the lacy tubeworm *F.implexa*, the marine worm *Myxicola* and the encrusting sponge of the genus *Lophon* seem to form a distinct community with *D.vexillum*. Conversely species such as barnacles of the genus *Balanus*, the Atlantic sea scallop (*P.magellanicus*), the tube anemone of the genus *Cerianthus*, the green sea urchin (*S. droebachiensis*), and mussels of the family *Mytilidae* negatively correlate to *D.vexillum*. It is important to note that the majority of species which negatively

associate with *D.vexillum* are also less abundant in the area open to fishing since these species are more sensitive to disturbances due to bottom-fishing (Asch & Collie 2008). Other studies have shown that disturbed habitat is more susceptible to invasive species (Lozon & MacIsaac 1997, Marvier et al. 2004). The results from this study appear to support this hypothesis since the open area disturbed by bottom-fishing is more heavily invaded. Furthermore, *D.vexillum* may be more abundant in the open area since fishing vessels are likely a vector for its spread (Herborg et al. 2009); dredging may fragment colonies that can attach to fishing gear and further its spread in the benthos. Therefore, the disturbance caused by dredging and commercial fishing vessels acting as a vector for its spread may interact to introduce and then allow *D.vexillum* to proliferate in the more disturbed habitats. However, once the area has been invaded by *D.vexillum*, its presence, rather than the process of bottom-fishing is likely the strongest driver of biodiversity decline.

Since several species analyzed in this study have a negative correlation with the presence of *D.vexillum*, there may be a decline in the abundance of members of the invertebrate community in areas infested with *D.vexillum*. Alterations to the benthic habitat on Georges Bank due to *D.vexillum* may also affect productivity of fisheries in the region since the gravel habitat it prefers is also habitat for juvenile fishes and scallop spat, though more research is necessary to determine this invasive species' impact on fishery productivity. Predators of *D.vexillum* include sea urchins (*Strongylocentrotus droebachiensis* and *Strongylocentrotus franciscanus*), although in experimental tests these predators prefer other food sources when available (Epelbaum et al. 2009). Unexpectedly, the green sea urchin (*Strongylocentrotus droebachiensis*) was found to be negatively correlated to *D.vexillum* and is not part of its community cluster in either open or closed area PCAs when *D.vexillum* is present. Another study in New Zealand indicated that sea

star and sea urchin predators may limit the spread of *D.vexillum* (Forrest et al. 2013), although the species of predators examined in these studies are not found on Georges Bank. Therefore the spread of *D.vexillum* on Georges Bank may at least be partially due to the lack of natural predators and competitors, supporting the enemy-release and competitive-release hypotheses (Liu & Stiling 2006; Blossey & Notzold 1995).

The lacy tubeworm *F.implexa*, was found to positively associate with *D.vexillum* and is part of the same community in the multivariate analysis. Consistent with other studies, encrusting taxa such as the lacy tubeworm have been found in disturbed shallow habitat in high densities and are known as early colonizers (Asch & Collie 2008, Collie et al. 2009). The lacy tubeworm may also have a relationship with the *Cancer* crabs, since crab species are also known to utilize the calcareous tubes the lacy tube worms produce as habitat to reduce risk of predation (Heck & Hambrook 1991). The calcareous tubes created by serpulid polychaetes are modified by environmental factors (Bornhold & Milliman 1973); thus the presence of *D.vexillum*'s acidic tissues in the environment may alter the chemical environment that these species use to create calcareous tubes, which serve as habitat for several other species. Furthermore, laboratory experiments have indicated that *Cancer* crabs can prey on other species of solitary ascidians such as *Ascidiella aspersa*, *Ciona intestinalis*, and *Styela clava* but not on colonial ascidians such as *D.vexillum* (Dijkstra & Harris 2007).

Bottom-fishing also appears to restructure some associations among species as found in our multivariate analysis. Specifically sea stars of the genus *Asterias* and the crab *C.borealis* were more closely associated with species found in the *D.vexillum* community in the open areas whereas these species were not associated with the *D.vexillum* group in the closed areas (Figure 3.5). Sea stars of the genus *Asterias* were also found to be more abundant at disturbed sites in



high gravel habitat (Figure 3.6), which may be explained by the fact that they scavenge and have been reported to feed on organisms damaged by bottom-fishing (Ramsay et al. 1998, Jenkins et al. 2004). Sea stars may be tolerant of *D.vexillum* tissues as demonstrated by their close spatial association in HabCam images (Figure 3.4). Moreover, sea star predation as well as intra and interspecific interactions among sea stars have been shown to affect the distributions of invertebrate prey species (Gaymer et al. 2004, Shank et al. 2012).

The most motile species analyzed in this study are the *Cancer* crabs and their motility may enable them to inhabit and traverse areas infested with *D.vexillum* without having a significant negative impact on their distribution in these areas. Moreover, *Cancer* crabs are scavengers that may colonize disturbed habitats and consume prey items damaged or discarded from bottom-fishing (Collie et al. 2009). Studies have shown that they utilize chemical cues to detect, locate and identify food items (Rebach 1996); thus the presence of discards and prey items damaged by bottom-gear may attract these crabs to the open area. Scavengers including *Cancer* crabs and *Asterias* sea stars in the Irish Sea have been shown to aggregate around damaged scallops in particular, having implications for an increase in incidental scallop mortality caused by dredge gear (Jenkins et al. 2004). *Cancer* crabs have also been shown to break open even lightly damaged scallop shells (Jenkins et al. 2004). Therefore, *Cancer* crabs higher abundance in the open area may be explained by greater access to food resources as a result of fishing.

Bottom-fishing may alter interactions among species that together drive variation among the sites as observed in the PCA. The clustering among three species groups identified in both closed area PCAs appears more diffuse and not as tightly clustered in the open area PCAs (Figure 3.5). Species may associate with each other to form mutualistic relationships that serve

an ecological purpose such as predator avoidance in the case of *Cancer* crabs using calcareous tubes formed by the lacy tubeworm *F.implexa* (Heck & Hambrook 1991), although this relationship may be altered in the presence of bottom-fishing if these tubes are crushed. Generally, scallop dredging on Georges Bank creates a high level of disturbance as compared to natural disturbances created by storm events (Jennings & Kaiser 1998). Previous research has shown that areas impacted by bottom-fishing are found to have lower abundance of organisms, lower species richness and lower diversity as compared to areas that are undisturbed (Collie et al. 1998, Asch & Collie 2008). Additionally, bottom-fishing affects the physical structure of the benthos and benthic community functional groups (Tillin et al. 2006, Hinz et al. 2009). Heavily trawled areas have been found to have greater abundances of motile animals, as well as infaunal and scavenging invertebrates, while attached filter-feeding, and larger more sedentary animals are more abundant in areas with lighter trawling effort (Tillin et al. 2006). These findings are consistent with our results when examining pooled data based on open and closed areas, though area as a factor did not have a significant effect on the decline in biodiversity as measured by the Shannon index per site, which was driven primarily by *D.vexillum*.

Studies conducted in the Gulf of Alaska and Irish Sea show that most motile organisms are less severely affected by chronic and experimental trawling than anthozoans, sponges, bryozoans, tubicolous polychaetes and barnacles (Freese et al. 1999, Bradshaw et al. 2002). Species with softer tissues are more vulnerable to bottom-fishing impacts as compared to encrusting species (Asch & Collie 2008). In this study encrusting sponges of the genus *Lophon* were more abundant in the open area than the closed area whereas globular sponges of the genus *Polymastia* demonstrated the opposite relationship since their softer tissues may make them more sensitive to bottom-fishing impacts (Asch & Collie 2008). The effects of bottom-fishing may be

cumulative, therefore small-scale experimental studies cannot capture large scale spatial and temporal trends that can be extrapolated to the ecosystem level (Hinz et al. 2009). In contrast to small-scale experimental studies, this observational study evaluates a large area in situ providing detailed observations of ecological interactions in the northern edge of Georges Bank, though more data is needed to evaluate trends over time.

*Didemnum vexillum* may also be more widespread in habitat disturbed by dredging since disturbed habitats are generally more susceptible to invasive species (Lozon & MacIsaac 1997, Didham et al. 2007b). Closed areas contain higher levels of biodiversity as measured by the Shannon index in comparison to dredged areas when sites were pooled by area. Therefore, the higher biodiversity in this area may make it less susceptible to invasion, which is consistent with the insurance hypothesis; higher biodiversity leads to lower susceptibility to invasive species since there are fewer resources available in the more biodiverse area for the invasive to exploit (Yachi & Loreau 1999, Stachowicz et al. 1999, Marraffini & Geller 2015). *Didemnum vexillum* is also present in the closed area, albeit at lower densities than the open area, though its presence there also has a strong impact in driving variation among sites. *Didemnum vexillum* appears to be a key driver of ecological change in the study area regardless of disturbance regime, which is consistent with other studies supporting the driver hypothesis of invasive species impacts on native communities (Light & Marchetti 2007). The area effect, representing different levels of disturbance from bottom-fishing processes, was not significant in affecting the Shannon index as measured per site, which would be expected to show a significant effect if bottom-fishing was a driver of biodiversity loss as indicated in the passenger and back-seat driver hypotheses (Bauer 2012; MacDougall & Turkington 2005). Therefore, the results from this study are most consistent with the driver hypothesis in characterizing the effects of this invasive species on

biodiversity.

In this study we examined interactions of an invasive tunicate *D.vexillum* with other species of the invertebrate community on Georges Bank and found it appears to restructure the invertebrate community when present. This study demonstrates the impact of this invasive tunicate is stronger in altering the ecological community and biodiversity than the disturbance caused by bottom-fishing. Furthermore, we have demonstrated the extensive impacts an invasive species can have on benthic communities and biodiversity using advanced technology for observing a commercially important region over a large scale. Large scale in-situ studies comparing fished and protected areas provide valuable insights into understanding ecological interactions in these communities, which can be used to implement ecosystem-based strategies into marine management.

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## APPENDIX A: Chapter 1 supplementary materials

### *Governance and ecological data temporal considerations*

The following eight MPAs included ecological data from sites collected after 2000: Biscayne National Park, Culebra National Wildlife Refuge, Florida Keys National Marine Sanctuary, Dry Tortugas National Park, John Pennekamp Coral Reef State Park, Parque Nacional Marino Punta Frances, Parque Nacional Jaragua and Parque Nacional Marino Bastimentos (Table 2). The time of collection of ecological indicators and governance data collection in 1999 were researched to determine if MPA management regulations had changed in this time period. (Roman 2012). Monitoring and enforcement of the Florida Keys National Marine Sanctuary during the collection of the ecological data in this study was conducted by the Florida Fish and Wildlife Conservation Commission which began in 1997 acting in partnership with NOAA law enforcement in accordance with the Florida Keys National Marine Sanctuary code of Federal regulations which were in effect through the time of the AGRRA surveys (*National Marine Sanctuary Act 1997 sec. Subpart P=Florida Keys National Marine Sanctuary, “Florida Keys National Marine Sanctuary Revised Management Plan, 2007” n.d.*). Biscayne National Monument was re-designated as a national park and expanded in 1980 (Public Law 96-287) and the comprehensive general management plan formed in 1983 for the park was active for the time of the governance and AGRRA surveys used in this study (National Park Service, U.S. Department of Interior 2015). Culebra National Wildlife Refuge, Puerto Rico, during the time of governance data collection and AGRRA surveys was managed by the Department of Natural and Environmental Resources in Puerto Rico (DNER) operating under the Fisheries and Wildlife

Strategic Plan 1996 and enforced by the Puerto Rico DNER law enforcement division during the governance and ecological surveys used in this study. The Dry Tortugas National Park regulations were implemented by the U.S. National Park Service established in 1992 established by Public Law 102-525 under which regulations were overseen during the time of the governance survey and ecological data collection. The John Pennekamp Coral Reef State Park during this time period operated under the 1998 management plan which was not replaced until 2004, after the governance and AGRRA survey data collected for this project were collected (“John Pennekamp Coral Reef State Park Approved Management Plan” 2004). The Parque Nacional Marino Punta Frances in Cuba was governed as part of the National System of Protected Areas under the Decree-Law 201/1999, which established regulations with regard to the administration and control defining protected area categories for Cuba and regulated the level and types of use allowed in protected areas including regulations for control, management, funding and administration (Angulo-Valdés 2005). This law was active during the period of governance survey data collection and AGGRA survey data collection (Angulo-Valdés 2005). Parque Nacional Jaragua in the Dominican Republic was created in 1983 and management was updated in 2000 under the General Law of the Environment and Natural Resources No. 64 and the Law of Protected Areas No. 202 in 2004 (Perdomo, L. et al. 2010), however the management strategy was not updated until 2005 after this study time period (“Guía Metodológica para la Elaboración y/o Actualización de Planes de Manejo de Áreas Protegidas de República Dominicana. Santo Domingo, República Dominicana.” 2005). Parque Nacional Marino Bastimentos in Panama is governed under the General Law of the Environment No. 41 enacted in 1998 and administered by the National Authority of the Environment (Autoridad Nacional del Ambiente) during the collection of governance and ecological data used in this study (“Estado de



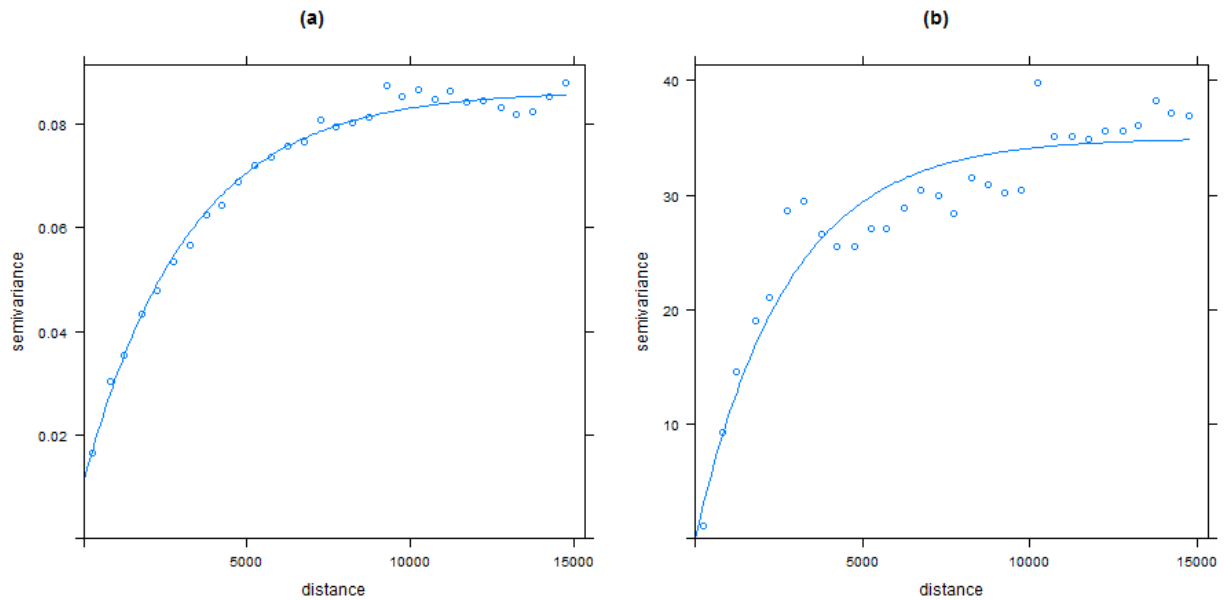
la Gestion Compartida de Areas Protegidas en Panama” 2006).

Table A1. List of the 21 MPAs analyzed in this study by country, year established, marine area and the number of AGRRA sites with ecological data within the MPA.

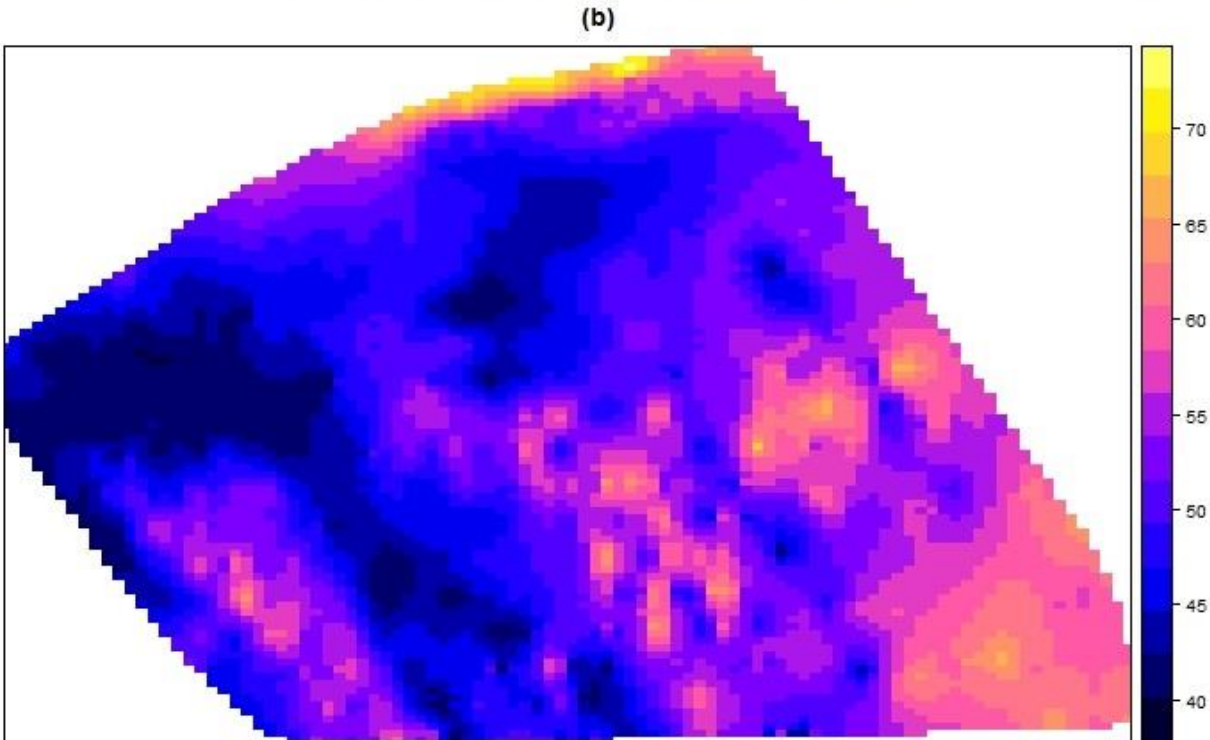
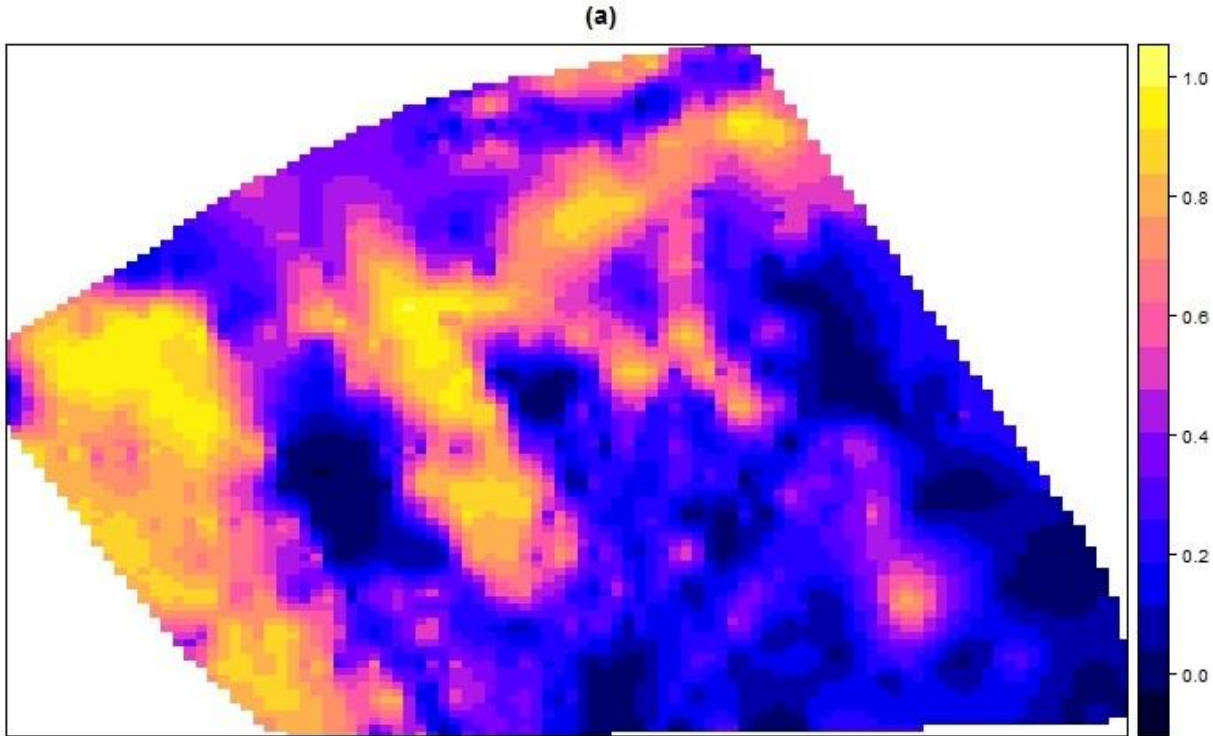
MPA	Country (Region)	Year established	Marine Area (km <sup>2</sup> )	Number of AGRRA sites	Year of AGRRA survey
Biscayne National Park	USA (Florida)	1969	728.43	6	2003
Culebra National Wildlife Refuge	USA (Puerto Rico)	1909	0.5	3	2003
Dry Tortugas National Park	USA (Florida)	1935	261.87	16	2004
Florida Keys National Marine Sanctuary	USA (Florida)	1990	9515	21	2003
Flower Garden Banks National Marine Sanctuary	USA (Texas)	1992	145.04	2	1999
Glover's Reef Marine Reserve	Belize	1996	308	10	2000
John Pennekamp Coral Reef State Park	USA (Florida)	1959	217.05	8	2003
Montego Bay Marine Park	Jamaica	1992	15.3	5	2000
Ocho Rios Protected Area	Jamaica	1966	133.186	3	2000
Parque Nacional Marino. Punta Frances	Cuba	1996	11	4	2001
Parque Nacional Cahuita	Costa Rica	1970	10.68	3	1999
Parque Nacional Jaragua	Dominican Republic	1983	0.91	1	2004
Parque Nacional Marino	Panama	1988	132.26	4	2002

Bastimentos					
Parque Nacional Sur de Guanahacabibes	Cuba	1997	90	4	1999
Reserva de la Biosfera Sian Ka'an	Mexico	1986	1200	12	1999
Reserva Especial de la Biosfera Isla Contoy	Mexico	1961	48.96	10	2000
Saba Marine Park	Netherlands	1987	8.7	7	1999
Salt River Bay National Historical Park and Ecological Preserve	US Virgin Islands	1992	2.43	1	1999
South Water Cay Marine Reserve	Belize	1996	477.01	1	2000
Tobago Cays National Marine Park	Saint Vincent and the Grenadines	1987	50	5	1999
United States Virgin Islands National Park	US Virgin Islands	1962	22.87	6	1999
Total				132	

APPENDIX B: Chapter 2 supplementary information

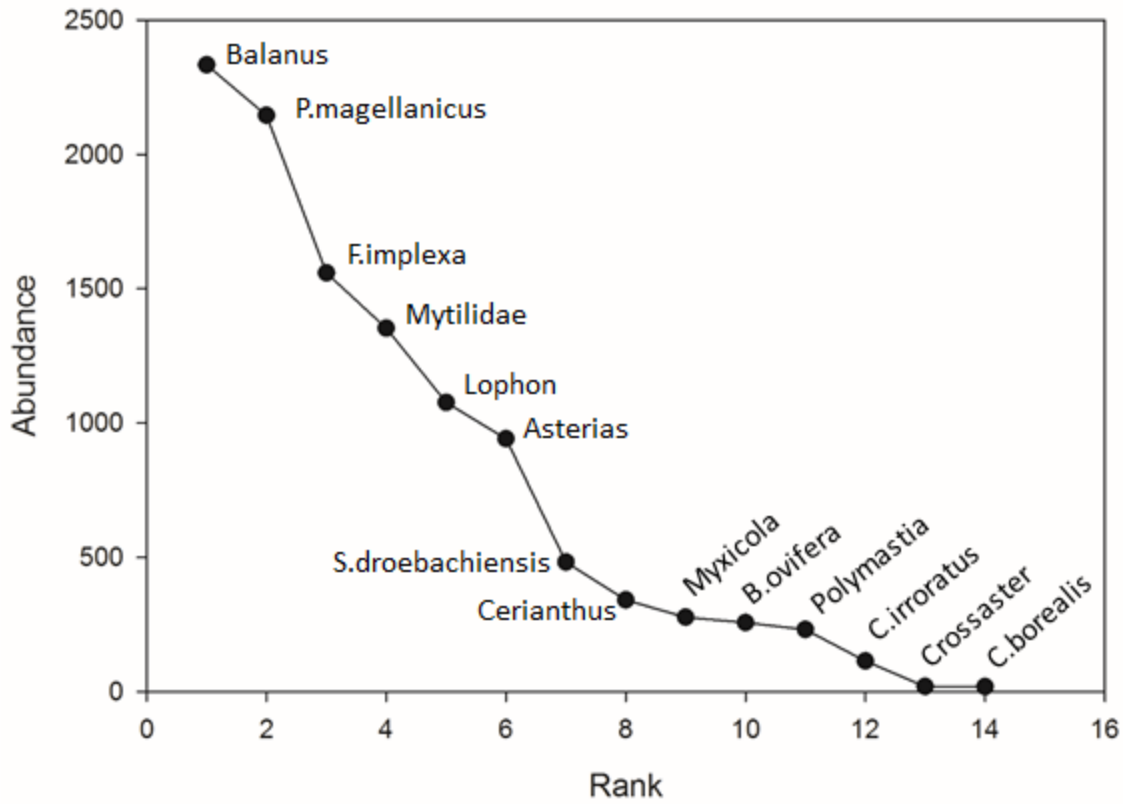


S1 Appendix B. Variogram model fits for (a) Gravel using the exponential model and (b) Depth also using the exponential model.



S2 appendix B. (a) Gravel proportional cover over study area based on ordinary kriging estimates. (b) Depth (m) based on ordinary kriging estimates. Kriged estimates were used to create prediction grid for *D.vexillum* distribution.

APPENDIX C: Chapter 3 supplementary information



S1 Appendix. Rank abundance plot of all count species found in the study area.