Marine Bioinvasions in Anthropogenic and Natural Habitats:
an Investigation of Nonindigenous Ascidians in British Columbia

by

Christina Simkanin
B.Sc., University College Cork, 2002
M.Sc., Galway-Mayo Institute of Technology, 2004

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Supervisory Committee

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The simultaneous increase in biological invasions and habitat alteration through the building of coastal infrastructure is playing an important role in reshaping the composition and functioning of nearshore marine ecosystems. This thesis examined patterns of marine invasions across anthropogenic and natural habitats and explored some of the processes that influence establishment and spread of invaders. The goals of this thesis were four-fold. First, I examined the habitat distribution of marine nonindigenous species (NIS) spanning several taxonomic groups and geographical regions. Second, I conducted systematic subtidal surveys in anthropogenic and natural habitats and investigated the distribution of nonindigenous ascidians on Southern Vancouver Island, British Columbia, Canada. Third, I tested methods for in-situ larval inoculations and utilized these techniques to manipulate propagule supply and assess post-settlement mortality of ascidians across habitat types. Fourth, I investigated the role of biotic resistance, through predation by native species, on the survival of ascidian colonies in anthropogenic and natural habitats.

Results from this research showed that anthropogenic habitats are hubs for marine invasions and may provide beachheads for the infiltration of nearby natural sites. Specifically, a literature review of global scope showed that most NIS are associated with anthropogenic habitats, but this pattern varied by taxonomic group. Most algal and mobile invertebrate NIS were reported from natural habitats, while most sessile NIS were reported from artificial structures. Subtidal field surveys across both anthropogenic and natural habitats showed that nonindigenous ascidians were restricted largely to artificial structures on Southern Vancouver Island and that this pattern is consistent across their global introduced ranges. Field manipulations using the ascidian *Botrylloides violaceus* as a model organism, showed that post-settlement mortality is high and that large numbers of larvae or frequent introduction events may be needed for successful initial invasion and successful infiltration of natural habitats. Experiments also showed that predation by native species can limit the survival of *B. violaceus* in anthropogenic and natural habitats. This dissertation contributes knowledge about the patterns and processes associated with habitat invisibility; provides insight into factors affecting colonization; and supplies valuable information for predicting and managing invasions.

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Dedication

For my mom, Patricia, and my daughter, Elsa.

Chapter 1: Introduction

1.1 Biological Invasions

Biological invasions result from the arrival of propagules and the establishment of a species beyond its native geographical range. The anthropogenic translocation of species began thousands of years ago as human populations traversed land and sea (Mills et al. 1993); however, as globalization has increased in recent time, the rate of invasions has increased dramatically (Cohen and Carlton 1998; Ruiz et al. 2000). Although the presence of nonindigenous species (NIS) has been observed for centuries (Chew 2011), the significance and impact of these species was not widely recognized until relatively recently (Elton, 1958, Drake et al. 1989). In recent decades, invasion biology has become an important multi-disciplinary field of ecology (Richardson and Pyšek, 2008). Studying biological invasions can contribute to the understanding of fundamental ecological and evolutionary processes as these large scale biogeographic 'experiments' can provide otherwise unattainable insights. Knowledge of the patterns and processes of invasions has contributed to the study of competition, biotic resistance, environmental suitability, phenotypic plasticity, evolution, genetic processes and factors that affect species range and population size limits (Grosholz 2002; Sax et al., 2007; Blackburn 2008; Geller et al. 2010).

The consequences of species' invasions vary enormously and not all of them have negative or detrimental socio-economic and/or environmental effects. In fact, many introduced species have no detectable impact on their receiving environment; and in some cases, scientists have argued that by adding to the biodiversity of a new region these species actually have a positive impact (Sax and Brown, 2000). However, a subset of the species that are introduced, freed of the natural controls in their native range, proliferate and invade natural systems, displace native species, and degrade ecosystem services important to human economies (Vitousek et al., 1996; Pimentel et al., 2005; Colautti et al. 2006). These species are referred to as "invasive" species. It is this subset of species that have rightly earned NIS the title as one of the greatest environmental and economic threats to native ecosystems (Wilcove et al., 1998; Simberloff et al. 2013). For instance, in its introduced range on the east coast of North America the marine crustacean *Carcinus maenas* alters community structure by preying on native gastropods, bivalves and other crabs (Vermeij 1982; Grosholz and Ruiz 1996) and has been associated with the demise of the soft-shell clam (*Mya arenaria*) industry, causing a loss of nearly $44 million/year (Lafferty and Kuris, 1996; Pimentel et al. 2005). In addition to documenting ecological and economic impacts of this species, studying the *C. maenas* invasion has provided insight into the biotic (deRivera et al. 2005) and abiotic (deRivera at al. 2011; Kelly et al. 2011) processes limiting species biogeographical ranges.

1.1.1 Stages of Invasion

To reduce the likelihood of detrimental NIS colonizing and spreading to new areas we must understand the process of invasion. This requires an examination of the vectors transporting species, the factors that influence establishment success of an invader, and the dynamics that control the ultimate distribution of NIS once they are established. Invasion is considered a multistep process and has been characterized as a series of stages (Carlton, 1985; Williamson and Fitter, 1996; Richardson et al. 2000; Kolar and Lodge, 2001; Colautti and MacIsaac, 2004). Although the terminology used to describe the stages has varied by author (see review in Blackburn et al. 2011), they are essentially: transport, introduction, establishment and spread. Each stage is not completely distinct but they represent biologically identifiable steps along the path to becoming an invader (Lockwood et al. 2007).

The anthropogenic invasion process begins in a species' native habitat where they are entrained by a transport pathway (e.g. cargo on a commercial ship) and carried beyond their natural biogeographical boundaries. This transport event terminates at a new location where propagules (e.g. adults, larvae, seeds, etc.) are introduced. Once dispersed these propagules face the abiotic and biotic conditions of the receiving environment and may become established. After establishing, an invader may begin to propagate and spread beyond the initial introduction location. Spread may occur through natural dispersal or a species may become entrained by another pathway and continue to spread to additional areas by the ‘stepping stone’ pattern of invasion that is characteristic of many NIS (Kolar and Lodge, 2001). Each stage is associated with a number of exclusion mechanisms or causes of mortality that determine the likelihood of a species passing from one stage to the next (Sakai et al. 2001; Blackburn et al. 2011). Thus, only a small fraction of transported organisms are expected to survive and persist through the whole invasion process to become established in a new environment (Williamson, 1996; Williamson and Fitter, 1996).

1.2 Marine Bioinvasions

In coastal environments, the observed rate of aquatic invasions has increased rapidly throughout the 20th century, and is continuing to increase with each passing decade (Cohen and Carlton, 1998; Ruiz et al., 2000; Ruiz et al., 2011). This rapid redistribution of species can be attributed to a suite of vectors, including shipping, aquaculture transfers, and recreational boating. The accelerating rate of global commerce and the subsequent rise in ship transport is considered the largest vector of marine invasions (Carlton, 1985; Ruiz et al. 2000; Gollasch, 2006). Commercial ships can entrain and carry species in ballast water (Carlton 1985) or transport species that are attached to hulls and sea chests (Carlton and Hodder, 1995; Coutts et al. 2003). Many marine species have life stages that can be carried by multiple vectors, either as planktonic larvae in ballast water or sessile or sedentary adult stages on ships hulls, recreational boats or shellfish aquaculture stock.

The transport of marine species beyond their native biogeographical boundaries has altered the natural mosaics of species in coastal environments. The magnitude of this process was illustrated by a study which found over 350 different species entrained in ballast water aboard cargo ships arriving into a single Oregon estuary (Carlton and Geller, 1993). Furthermore, the degree to which NIS have contributed to regional flora and fauna has been brought to the fore by a number of surveys that have highlighted the large number of NIS in different regions. For instance, an assessment of NIS in San Francisco Bay, California documented more than 200 species (Cohen and Carlton, 1998). Surveys of this kind have been carried out around the globe and have documented similarly high numbers of NIS in relatively small geographic areas, including 96 species in Pearl Harbor, Hawaii (Coles et al. 1999), 160 species in Port Phillip Bay, Australia (Hewitt et al. 2004), and over 500 species in the Mediterranean Sea (Galil, 2008).

1.2.1 The Role of Anthropogenic Structure

In an assessment of human-induced pressures on native species, Wilcove et al. (1998) found that habitat loss is the single greatest threat to biodiversity, followed by the spread of NIS. As coastal human populations have increased in size, nearshore environments have been rapidly modified to promote tourism, support commerce and protect shorelines from erosion and other environmental perturbations (Glasby and Connell, 1999; Chapman and Underwood, 2011). Specifically man-made structures such as marinas, ports, breakwalls, jetties and shoreline protections are becoming ubiquitous features of modern coastlines (Bulleri and Chapman, 2010). The environmental impacts of these anthropogenic habitats are only now beginning to be understood (Bulleri and Chapman, 2010; Chapman and Underwood, 2011).

Referring to terrestrial systems, Charles Elton (1958) noted that ‘invasions most often come to cultivated land, or land much modified by human practice’. As mentioned above, maritime vectors such as shipping, recreational boating and aquaculture transfers are known to disperse marine NIS propagules around the globe (Carlton & Geller, 1993; Naylor et al., 2001; Floerl and Inglis, 2005). These dispersal events often begin and end at man-made structures such as shipping ports, docks and oyster cages. Consequently, there is a growing perception that anthropogenic habitats are foci for marine invasions and may represent important “beachheads” for species’ establishment, facilitating their persistence and spread (Bulleri and Airoldi, 2005; Glasby *et al*., 2007). Currently, however, we know very little about the extent to which species are spreading from these introduction sites into nearby natural habitats, and if so, what mechanisms are allowing them to be successful in establishing populations in natural environments.

1.2.2 Marine Bioinvasions in British Columbia

The British Columbia (B.C.) coast spans a 1000 km range of complex geography and oceanography (Thomson, 1981). While many coastal regions of the province are considered remote and pristine, recent analysis shows that the marine environment is extensively, and in some places intensively, utilized by humans (Ban and Alder, 2008). This anthropogenic stress includes commercial and recreational fishing, aquaculture operations, shipping and cruise ship commerce, and marina development (Ban and Alder, 2008). As human impacts have increased throughout the province, so has the number of reported marine NIS (Levings et al. 2002). To date, there are 99 invertebrate, algal, fish and vascular plant NIS reported from B.C. marine waters (Levings et al. 2002; Gillespie, 2007; Gartner, 2011; Graham Gillespie, pers. comm.). The primary introduction pathways for these species are historical aquaculture imports and commercial shipping by both ballast water and hull fouling (Levings et al. 2002).

In B.C., a number of different habitat types are invaded by marine NIS, including intertidal beach, rocky shore, subtidal bedrock, mud flat, marsh, seagrass, and anthropogenic structure (e.g. marina floats and pilings) (Levings et al. 2002; Lu et al. 2005; Gillespie, 2007; Gartner, 2011; Choi, 2012). A recent synthesis of NIS in North America (Canada and the USA) shows that most established nonindigenous marine and estuarine species are associated with hard substrate habitats as adults (71% of 327 total species; Ruiz et al. 2009). The study was not able to distinguish between the numbers of NIS in anthropogenic and natural hard substrate habitats, however, and the authors show that man-made structures have especially high numbers of invaders. In B.C., patterns of NIS distributions in anthropogenic and natural habitats are also unknown. A recent study examined the broad-scale distribution of subtidal NIS throughout the province (Gartner, 2011), but most of the survey locations were man-made structures (e.g. marinas and buoys). To date, there has been no assessment of invasion patterns in anthropogenic and natural subtidal habitats and determining these trends is necessary for understanding the impact of NIS on native ecosystems. Further, knowledge of the distribution of NIS can help managers target prevention and eradication efforts, and can provide a baseline for carrying out ecological assessments which provide insight into the factors that affect establishment success.

1. 3 Nonindigenous Ascidians

Ascidians (Phylum Chordata, Sub-Phylum Tunicata, Class Ascidiacea) are diverse and abundant members of marine communities with approximately 3000 described species worldwide. They are hermaphroditic, sessile, filter feeding invertebrates that are found in a wide variety of habitats from shallow water to the deep sea (Millar, 1971; Monniot et al. 1991). They can be solitary or colonial in body form and have a complex life history with both a pelagic and sessile phase. During their pelagic larval phase, ascidians can actively disperse throughout the water column, before choosing a settling site and beginning metamorphosis to their sessile form (Svane and Young, 1989). They settle on a wide variety of substrates including rocky benthos, coral reefs, mangroves, algal fronds, soft sediments, bivalve shells and man-made structures (Millar, 1971; Lambert, 2005).

Around the globe, there are 64 ascidian species known to be nonindigenous in at least part of their documented range (Shenkar and Swalla, 2011). Some of these species are highly invasive with increased concern about their potential economic and ecological impacts (Lambert, 2007; McKindsey et al. 2007). For instance, a number of nonindigenous ascidians have been found to displace native species (Stachowicz et al. 2002; Castilla et al. 2004; Blum et al. 2007) and overgrow harvested aquaculture species (Carver et al. 2003, Rius et al. 2011). Many of these impacts are reported from anthropogenic habitats, such as marinas, docks, pilings, and aquaculture gear, where they appear to flourish (Lambert and Lambert, 1998; 2003; Lützen, 1999;Lambert, 2002; Lambert, 2005). Less is known about the distribution and potential impacts of these species in natural benthic systems (Lambert, 2005). Data from the few species known from these environments indicates that nonindigenous ascidians can greatly alter benthic community structure through competition with native species for space and resources (Castilla et al. 2004; Valentine et al. 2007).

1.3.1 Nonindigenous Ascidians in British Columbia

In B.C., there are six known nonindigenous and one cryptogenic (*sensu* Carlton 1996a) ascidian species. The six NIS include three solitary species: *Ciona savignyi* Herdman, 1882, *Molgula manhattensis* (De Kay, 1843), and *Styela clava* Herdman, 1882; and three colonial species: *Didemnum vexillum* Kott, 2002, *Botryllus schlosseri* (Pallas, 1766), and *Botrylloides violaceus* Oka, 1927. The cryptogenic colonial ascidian *Diplosoma listerianum* (Milne-Edwards, 1841) is widely distributed throughout the world and evidence suggests that it may represent a species complex (Fofonoff et al. 2013). In B.C., it was first reported in 1966 (Eldredge, 1966) and frequently it is found on man-made subtidal structures, however, because its native range is unknown and its taxonomy is not resolved it is considered cryptogenic throughout most of its range. Two of the six nonindigenous species have very limited distributions throughout the province. *Ciona savignyi* is abundant throughout nearby Puget Sound, Washington, but there are limited records of this species in B.C. (Lambert, 2003; Lamb and Hornby, 2005). *Molgula manhattensis* has been found in limited numbers at French Creek on Vancouver Island (Lambert, 2003) and one specimen was reported from a marina in Prince Rupert (Clarke Murray et al., 2011).

Research carried out in this thesis focuses on the four established and broadly distributed nonindigenous ascidians in B.C.: *S. clava*, *D.vexillum*, *B. schlosseri*, and *B. violaceus*. In particular, *B. violaceus* is utilized in Chapters 4 and 5 as a case-study species to investigate factors that affect establishment and colonization of sessile marine invertebrates. *Botrylloides violaceus* is a highly successful and widespread invader, found around the globe. It is native to the Northwestern Pacific, ranging from Southern China to Southern Siberia (Saito et al. 1981; Cohen, 2005). Populations are established on both the east and west coasts of North America (Lambert and Sanaymyan, 2001; Ramsay et al. 2008), in the Mediterranean (Streftaris et al. 2005), and around Western Europe

(Gittenberger, 2007; Minchin, 2007) and Australia (Dafforn, 2008). On the Pacific coast of North America, its introduced range now extends from Mexico to Southern Alaska (Lambert and Sanaymyan, 2001) and its first reported occurrence within this range is from Santa Barbara Harbor, California, in 1966 (Ruiz et al. 2011). In southern B.C., it was first recorded in 1992; however, it was reported from nearby Puget Sound, Washington, as early as 1977 (Cohen, 2005). It is has been found on anthropogenic and natural habitats, including aquaculture sites, marinas, recreational boats and algal fronds (Gartner 2011; Clarke Murray et al. 2011; White and Orr 2011). It can be a strong competitor for space, rapidly overgrowing primary and secondary habitat, and can quickly become competitively dominant over other invertebrate species (Berman et al. 1992; Dijkstra et al. 2007; Miller and Etter 2011). Propagules of *B. violaceus* can disperse naturally on small geographic scales through short-lived larval dispersal, and over larger scales through fragmentation of colonies (Bullard et al. 2007) and rafting on floating debris (Worcester, 1994). The species' broad geographical range suggests that natural spread is not its primary dispersal mechanism however, and recent genetic analysis suggests that human-mediated vectors such as recreational boating and aquaculture transfers are largely responsible for its regional distribution on the west coast (Bock et al. 2010).

1.4 Research Objectives and Thesis Overview

Two primary goals of invasion ecology include determining patterns of invasions across habitat types (Lonsdale et al. 1999; Chytrý et al. 2008; Davis 2009) and understanding which processes affect establishment success of arriving propagules (Williamson, 1996;Kolar and Lodge 2001). To this end, I use a combination of observational and experimental methods to investigate the connection between anthropogenic structures and natural subtidal habitats with regard to the establishment and spread of invasive ascidians. I examine global patterns of marine invasions (Chapter 2), local patterns of ascidian invasions (Chapter 3) and carry out experimental manipulations to determine which mechanisms, including initial inoculation size (Chapter 4) and release from predators (Chapter 5) are important for invasion success (Figure 1.1).

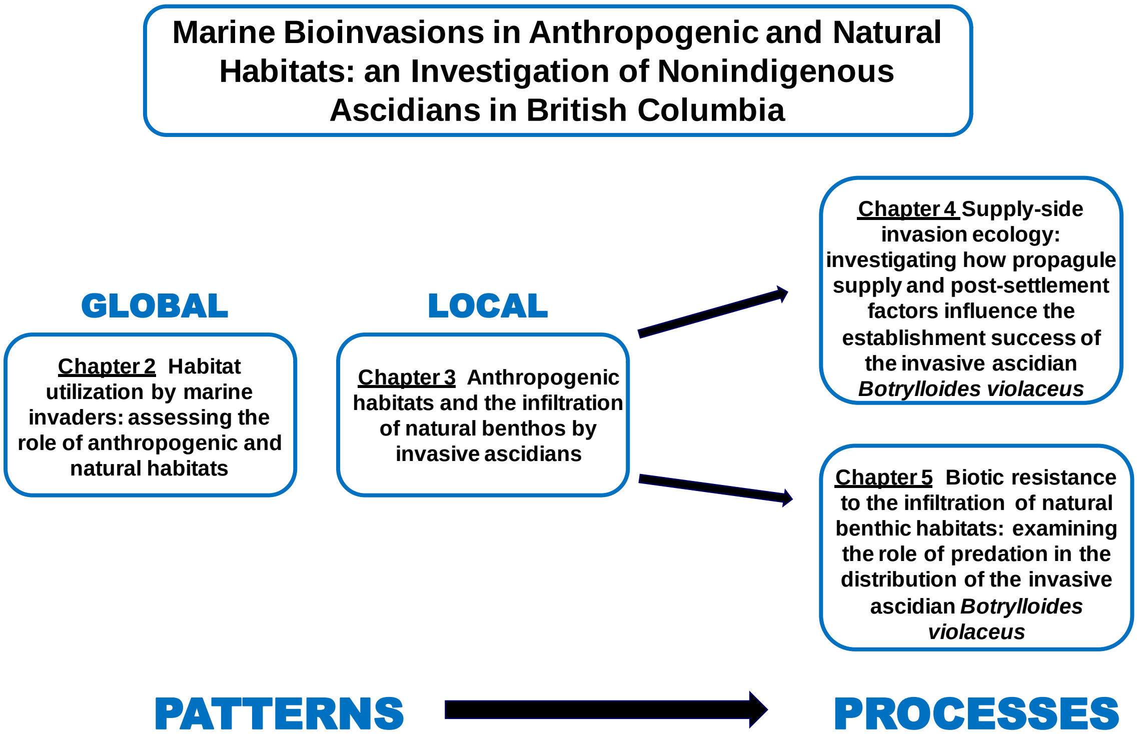

Figure 1.1: Organizational schematic of dissertation research.

Specifically, in Chapter 2 I review the marine invasion literature over a fifteen year period (1996-2010) to investigate the broad-scale distribution patterns of NIS between anthropogenic and natural habitats. There is a growing perception that anthropogenic structures are foci for marine invasions, but this view is based on localized studies of targeted taxa. This study was the first, to date, to assess the current state of knowledge across geographic areas and marine invertebrate and algal phyla. I also investigated how these observed patterns have been influenced by the choice of survey locations in marine invasion research.

In Chapter 3, I examine the distribution of four nonindigenous ascidians in marinas on Southern Vancouver Island, B.C. and the extent to which these species have successfully infiltrated nearby natural habitats. Anthropogenic habitats are highly susceptible to marine invasions, however, little is known about the extent to which these habitats may act as source populations for the spread of NIS into nearby natural habitats. I also assess the global habitat distribution of the four ascidian species to compare local distributional patterns with occurrence patterns across their native and introduced ranges.

In Chapter 4, I use *in-situ* experimental manipulations to test how propagule (i.e. larval) supply and post-settlement stressors interact to affect the establishment success of the invasive ascidian *B. violaceus* in floating (marina pontoons) and fixed (boulder) habitats. In two complimentary field experiments, I assess how propagule supply, settler density, habitat type, and access by predators affect survivorship of newly settled individuals. Testing these relationships provides critical insight into the factors that affect establishment, which is essential for predicting and managing invasions.

In Chapter 5, I delve into one of these factors, predation, in greater detail and test how biotic resistance affects establishment success. I conduct a series of predator exclusion experiments to determine whether predation by native species influences the successful infiltration of invasive ascidians into natural benthic habitats. This study utilizes the ascidian *B. violaceus* as a case study, but the results may have implications for the distribution of other high profile global invaders that are present in B.C.

In the final chapter (Chapter 6), I summarize the significant findings of my research and discuss how they contribute to the study and management of ascidian invasions specifically, but also invasions more generally. The research presented in this thesis (Chapters 2-5) was prepared as stand-alone manuscripts for publication. As such, there may be some redundancy across chapters. Two of the chapters (3 and 5) have been published.

Chapter 2: Habitat utilization by marine invaders: assessing of the role of anthropogenic and natural habitats

2.1 Abstract

The simultaneous increase in biological invasions and habitat alteration through the building of coastal infrastructure is playing an important role in reshaping the composition and functioning of near shore marine ecosystems. I investigated these interacting drivers of change to determine the distribution of nonindigenous species (NIS) among anthropogenic and natural habitats. I conducted a literature review of 15 years of publications on invertebrate and algal NIS from hard-bottom anthropogenic and natural habitats. There were 247 NIS reported in 707 distinct records from 270 papers that conducted NIS research on hard substrates. The literature review identified a pattern between habitat type and taxa type in studies of hard-bottom NIS, with differential patterns apparent for algal, mobile and sessile species. In anthropogenic habitats, sessile NIS were recorded more times and at a higher frequency than algae and mobile invertebrates. Results suggest that anthropogenic habitats are areas of high invasion success, especially for sessile species that tend to utilize novel surfaces (vertical, overhanging, and floating). Some sessile species have spread to natural habitats, but a majority appear restricted to man-made structures, whereas algal and mobile species exhibited the opposite pattern – being predominately reported from natural habitats. Ultimately, the patterns discovered during this study reflect both the actual distributions of NIS among habitats, and sampling bias by ecologists that can only be resolved using standardized (balanced) sampling protocols across habitats that are comparable among studies. Further investigation of the role of anthropogenic habitats as invasion sites and potential launching points for infiltration into natural habitats will provide insight into the factors affecting establishment and subsequent spread of NIS.

2.2 Introduction

The introduction and spread of nonindigenous species (NIS) is a major component of human-induced global change and plays a significant role in prompting the conservation of native habitats and the management of arriving species (Elton, 1958; Carlton, 1989; Mack et al. 2000). Although few ecosystems (if any) are free from invaders, not all regions and habitats are invaded by NIS to the same extent (Lonsdale, 1999; Chytrý et al. 2008). In marine environments, patterns of NIS establishment vary over latitudinal and regional scales. Trends show that temperate regions are invaded more frequently than polar regions (Ruiz and Hewitt 2008) and bays and estuaries are invaded more often than exposed open coasts (Wasson et al. 2005; Preisler et al. 2009; Ruiz et al. 2011). Within regions, levels of invasion can vary between habitats (Wasson et al. 2005; Zaiko et al. 2007) suggesting that not all habitat types are susceptible to invasion to the same extent. A recent assessment of the habitat distribution of marine NIS in North America found that hard benthic habitats are highly invaded (Ruiz et al. 2009), but a comparison of invasions across anthropogenic and natural habitats was not possible. Determining the patterns of habitat utilization by NIS is essential to predicting invasions, understanding invasion dynamics, detecting the conservation impacts of marine invasions and informing management strategies.

As globalization and trade continue to expand, novel anthropogenic habitats such as docks, wharves, pilings, seawalls, floating pontoons, riprap and aquaculture instillations are becoming ubiquitous features of developed coastlines. These anthropogenic habitats are increasingly built to support major vectors of biological invasions, including shipping, boating and aquaculture activities (Glasby and Connell, 1999; Bulleri and Chapman, 2010). Furthermore, in response to global changes, such as sea-level rise and increased storm frequency, coastal defense structures are frequently created to protect vulnerable coasts (Airoldi et al. 2005; Bulleri and Chapman, 2010). As man-made structures are continually added to coastal environments, it is important that we understand how these habitats function in the environment and how they may affect natural benthic ecosystems.

Anthropogenic and natural habitats differ in a number of physical characteristics, including the material from which they are constructed, and their surface topography and orientation (Chapman, 2003; Knott et al. 2004; Clynick et al. 2009). These physical properties can influence greatly the composition of marine communities (Pomerat and Reiner, 1942; Glasby, 2000) and research has shown that anthropogenic habitats often have different species assemblages than those in adjacent natural rocky habitats (Butler and Connolly, 1996; Glasby, 1999a; Connell and Glasby, 1999; Connell, 2001; Bulleri and Chapman, 2004; Clynick et al. 2008). For example, anthropogenic environments such as intertidal seawalls, which often have homogeneous surfaces with limited micro-habitats, support lower numbers of mobile species (Chapman 2003) and greater amounts of algae (Bulleri and Chapman, 2004) than adjacent rocky shores. Shaded man-made subtidal habitats such as marina pilings, often support a lower abundance of algal species and a greater abundance of sessile species such as ascidians, bryozoans and sponges (Glasby, 1999a,b).

Marine NIS are transported across biogeographical boundaries by a number of vectors including commercial shipping, recreational boating, and aquaculture transfers (Carlton, 1985; Ruiz et al. 2000; Naylor et al. 2001; Gollasch, 2006). Many of these long-distance, human-mediated dispersal events begin and end in close proximity to anthropogenic habitats. As vectors of NIS and anthropogenic habitats directly interact during the invasion pathway, the association between these habitats and NIS has long been known (Chapman, 1988; Chapman and Carlton, 1991). Furthermore, the stepping-stone spread or the movement of a NIS from one anthropogenic habitat to another is well documented (Glasby and Connell, 1999; Apte et al. 2000; Darling and Folino-Rorem, 2009; Floerl et al. 2009b; Goldstein et al. 2010). Although there is a clear link between anthropogenic structure and the distribution of NIS, little is known about whether many marine NIS are restricted to these types of habitats or whether they are equally distributed in natural benthic systems. A handful of studies have systematically compared the distribution of NIS in both anthropogenic and natural habitats (Lambert, 2002; Page et al. 2006; Glasby et al. 2007; Marins et al. 2010) and found that there were more NIS on artificial structures than on natural rocky reefs. These studies were limited in geographic and taxonomic scope, however, thereby hindering our overall understanding of the habitat distribution of marine NIS.

Most large-scale surveys for marine NIS target locations where vectors operate and where anthropogenic structures dominate, such as marinas or commercial shipping ports (Campbell et al. 2007). Comparatively little is known about the distribution patterns of marine NIS in natural habitats, even those directly adjacent to anthropogenic ones. Here I carried out a review of the published literature from 1996-2010 to investigate the distribution of NIS among anthropogenic and natural habitats. I compared the relative occurrence of NIS in different habitat types, using three categories of species: algae, mobile organisms, and sessile species, which allowed me to evaluate patterns across species groups. I also examined the extent to which anthropogenic and natural habitats are investigated by ecologists and how this affected the overall understanding of species distributions.

2.3 Methods

To identify papers conducting research on marine and estuarine NIS I carried out a systematic search of the published literature from 1996-2010 using the ISI Web of Science. The review targeted 39 ecology publications, including 17 marine journals, 15 general ecology journals, four multidisciplinary science journals, and three invasion biology journals (see Appendix A, Table A.1 for journal titles). Two of the journals, *Biological Invasions* and *Aquatic Invasions*, were not fully covered by Web of Science throughout the targeted timeframe and were searched directly via their respective websites. The initial search terms and their variants were: ‘nonindigenous’, ‘non-native’, ‘exotic’, ‘invasive’, ‘invasion’ and ‘introduced species’. I used the ‘topic’ search function to find these terms in the titles, abstracts and keywords of published papers. To further refine the results, I searched within the returned list of publications for the terms ‘marine’ or ‘estuarine’.

The search yielded 885 papers on marine and estuarine NIS. Within this list, a study was included in the analyses only if it met all three of the following criteria: (1) the study targeted nonindigenous invertebrate and/or algal species, (2) the study involved field-based research in hard substrate habitats (e.g. studies solely focused on laboratory experiments, genetics or vectors of NIS were not included), and (3) the study clearly stated the location and habitat type where organisms were sampled. The analyses were restricted to studies of hard substrates because anthropogenic structures are hard stable surfaces and comparisons with soft benthic and pelagic environments were deemed inappropriate for the aims of this study. Therefore, analyses included hard benthic associated organisms and excluded infaunal or planktonic organisms.

For each paper that met these criteria, both the methods and results sections were used to determine (i) the identity of invertebrate and algal NIS recorded, (ii) the type of habitats targeted for research (e.g. rocky benthos, marina piling, aquaculture gear), and (iii) the category of habitat from which NIS were recorded (i.e. anthropogenic or natural). Anthropogenic habitats were defined as man-made structures including piers, pilings, marina floats, break waters, rip-rap, and aquaculture gear. If a sampling apparatus (such as PVC tiles) was suspended from one of these structures, it was categorized as anthropogenic habitat. Natural habitat included the rocky intertidal, cobble beaches and subtidal rocky benthos. The distribution of NIS across anthropogenic and natural habitats was examined utilizing three categories of species: algae, mobile and sessile. I also assessed the frequency that habitat-species combinations were recorded, how often anthropogenic and natural habitats were targeted for sampling, and how many times each species was reported in the literature. This yielded comparisons of the numbers and frequencies of species recorded among habitats and the number of studies conducted across habitat types. Chi-square (χ^2) goodness of fit tests were used to test for significant differences between categories of species and habitats. All statistical analyses were performed in MINITAB 15.

2.4 Results

2.4.1 Species-habitat patterns

The literature search yielded 270 papers which conducted research on NIS in hard substrate habitats. Within these, a total of 247 NIS, distributed across 13 phyla, were reported (see Appendix ATable A.2 for species list). Phlya with the greatest NIS richness included the Arthropoda with 69 species, Chordata (ascidians) with 30 species, Ectoprocta (bryozoans) with 29 species, and Rhodophytes (red algae) with 29 species. More sessile species (119) were reported than either mobile (90) or algal (38) species.

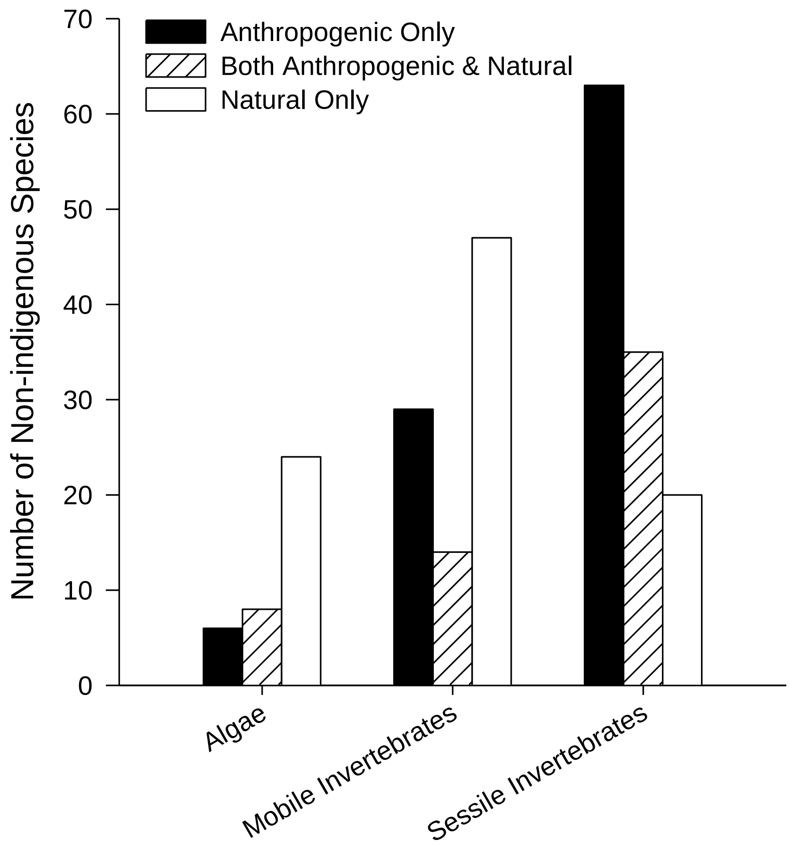

Figure 2.1:The number of algal, mobile and sessile invertebrate NIS recorded within anthropogenic or natural habitats from the 270 published research papers.

A greater proportion of species were associated with anthropogenic habitats (40%) than natural habitats (37%), while 23% of the NIS were reported as occurring in both. A total of 99 NIS (including algal, mobile, and sessile species) were reported from anthropogenic habitats only, compared to 92 NIS from natural habitats only. There were substantial differences in the distribution of algal, mobile, and sessile species across habitats. A majority of algal (63%) and mobile (52%) NIS were recorded in natural habitats only while just 17% of the sessile species were reported from natural habitats only (Figure 2.1). Sessile species were predominately reported from artificial habitats only (56% of species), versus 13% of algal and 32% of mobile species.

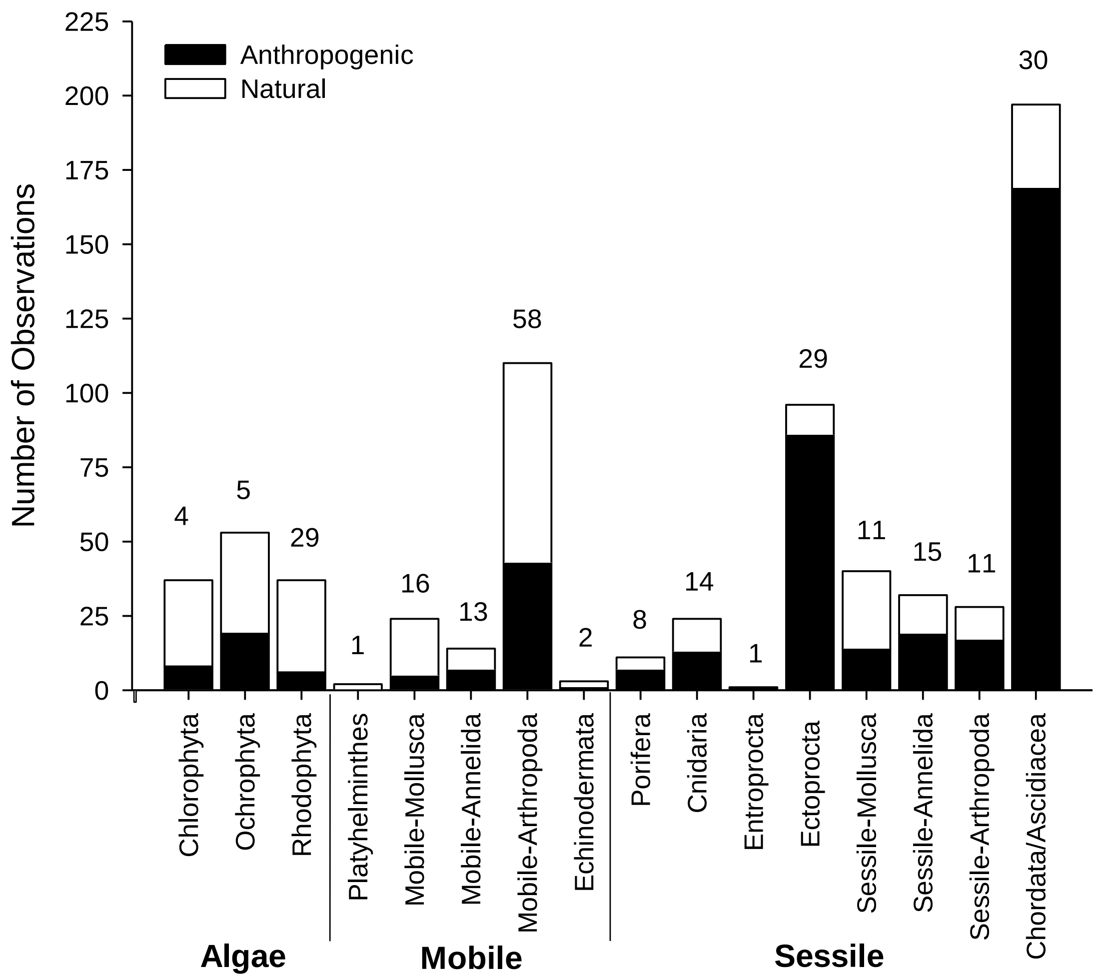

Figure 2.2:The number of times a species, arranged by phylum and taxonomic type (i.e. algae, mobile, or sessile), was observed in an anthropogenic or natural habitat. Numbers above the bars represent the total number of species in each group.

The distinctive pattern of sessile species tending to be more common in anthropogenic habitats was highlighted by a comparison of the number of times a species was observed in an anthropogenic or natural habitat. There were a total of 707 observation records for the 247 NIS. Algal and mobile species were observed more times in natural habitats than artificial ones (Figure 2.2). Sessile species, however, had a higher number of observation records from anthropogenic habitats than natural habitats (except for sessile molluscs). For example, of the 96 observations of nonindigenous bryozoans in the published literature, 90% were from anthropogenic habitats. Similarly, ascidians which were documented more than any other phylum (197 observations; Figure 2.2), were largely recorded on anthropogenic substrates (86% of records).

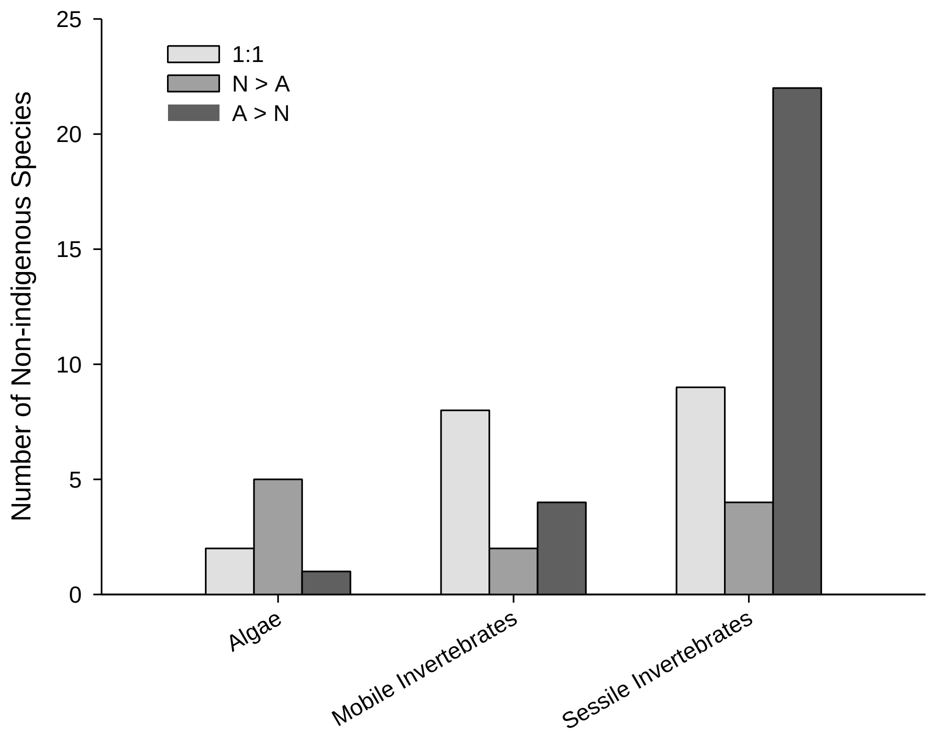

Figure 2.3:Nonindigenous species recorded in both habitats types (hashed bars Figure 2.1, n = 56). The bars represent the number of algal, mobile and sessile species recorded in natural and anthropogenic habitats in a 1:1 ratio, predominantly in natural habitats (N > A) or predominantly in anthropogenic habitats (A > N).

In total, 56 species where reported from both anthropogenic and natural habitats. This included eight algal species (21% of the total algal NIS), 14 mobile species (16% of the total mobile NIS), and 34 sessile species (29% of the total sessile NIS). Algal species reported from both habitat types were recorded more often in natural habitats than anthropogenic ones, while mobile invertebrates were reported from natural and anthropogenic habitats equally, and sessile invertebrates were reported more often in anthropogenic habitats (Figure 2.3). The only significant species – habitat combination was between sessile species and anthropogenic habitats (χ^2 = 14.8, d.f. = 2, p < 0.001). Twenty-two sessile species were reported more frequently from anthropogenic habitats than from natural ones. In comparison, only four sessile NIS were reported more often in natural habitats.

2.4.2 Sampling patterns

A majority of the 270 papers carried out research solely in natural habitats (55%). A further 33% conducted research solely in anthropogenic habitats, while the remaining 12% included some sampling in both. A number of different anthropogenic and natural habitats were targeted for study (Figure 2.4). The dominant natural habitats targeted were intertidal and subtidal rock, while marina docks and artificial rock (i.e. break waters and rip-rap) were the dominant anthropogenic habitats targeted.

There was a striking interaction between sampling effort (number of studies) in anthropogenic habitats and types of organisms recorded (Figure 2.5). There were four times the number of studies that targeted anthropogenic habitats (only) and recorded sessile invertebrates compared to mobile invertebrates or algae (χ^2 = 60.74 , d.f. = 2, p < 0.001). In contrast, there was no significant difference in number of studies that targeted natural habitats (alone) and recorded algal, mobile, and sessile NIS (χ^2 = 1.876, d.f. = 2, p = 0.391). Studies that included sampling of both artificial and natural habitats were significantly fewer for algae and mobile species than for sessile species (χ^2 = 21.158, d.f. = 2, p < 0.001). Algal and mobile NIS were reported predominantly in studies targeting natural habitats (χ^2 = 60.96 , d.f. = 2, p < 0.001 and χ^2 = 39.5 , d.f. = 2, p < 0.001, respectively), and sessile NIS were reported predominantly from studies that targeted anthropogenic habitats ($\chi^2 = 25.04$, d.f. = 2, $p < 0.001$).

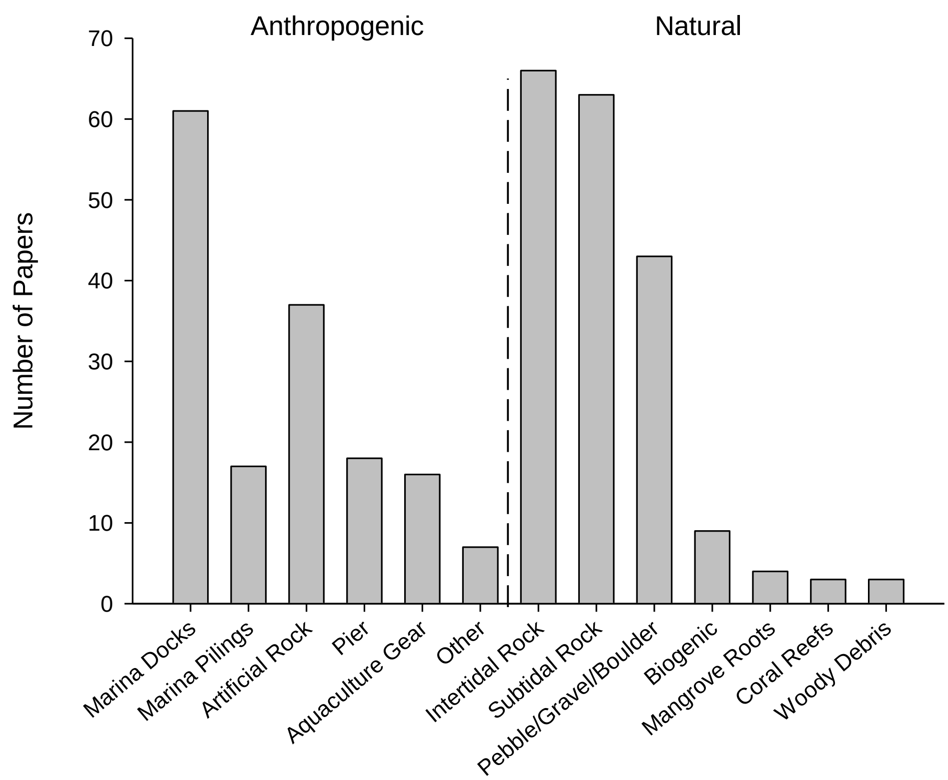

Figure 2.4:The type of habitat(s) targeted for field research within the 270 research papers that studied hard substrates. The data sums to greater than 270 because in some cases multiple habitat types were targeted.

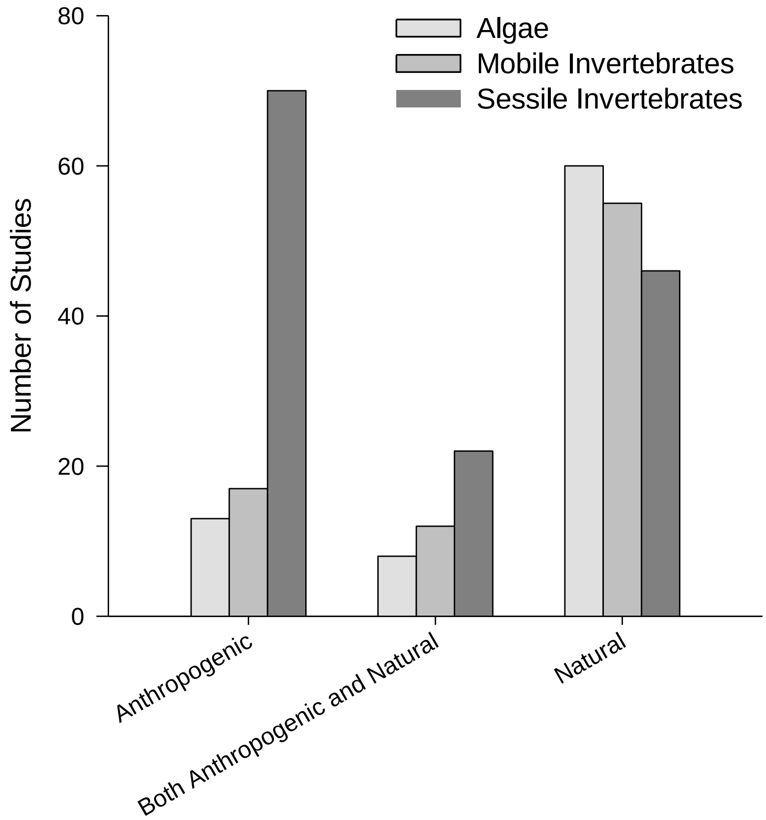

Figure 2.5:The number of studies targeting anthropogenic, natural or both habitat types that reported algal, mobile or sessile NIS. Data sums to greater than 270 because some studies recorded multiple species types.

Of the 707 separate observations of NIS, a majority of NIS were observed only once (154 species), but 93 NIS were observed multiple times (Figure 2.6). The most studied nonindigenous species of algae, *Sargassum muticum* (Yendo) Fensholt, 1955 was recorded in 24 papers; while the most studied mobile invertebrate, *Hemigrapsus sanguineus* (De Haan, 1835) was reported in 14 papers; and the most studied sessile invertebrate, *Botrylloides violaceus* Oka, 1927was reported in 29 papers.

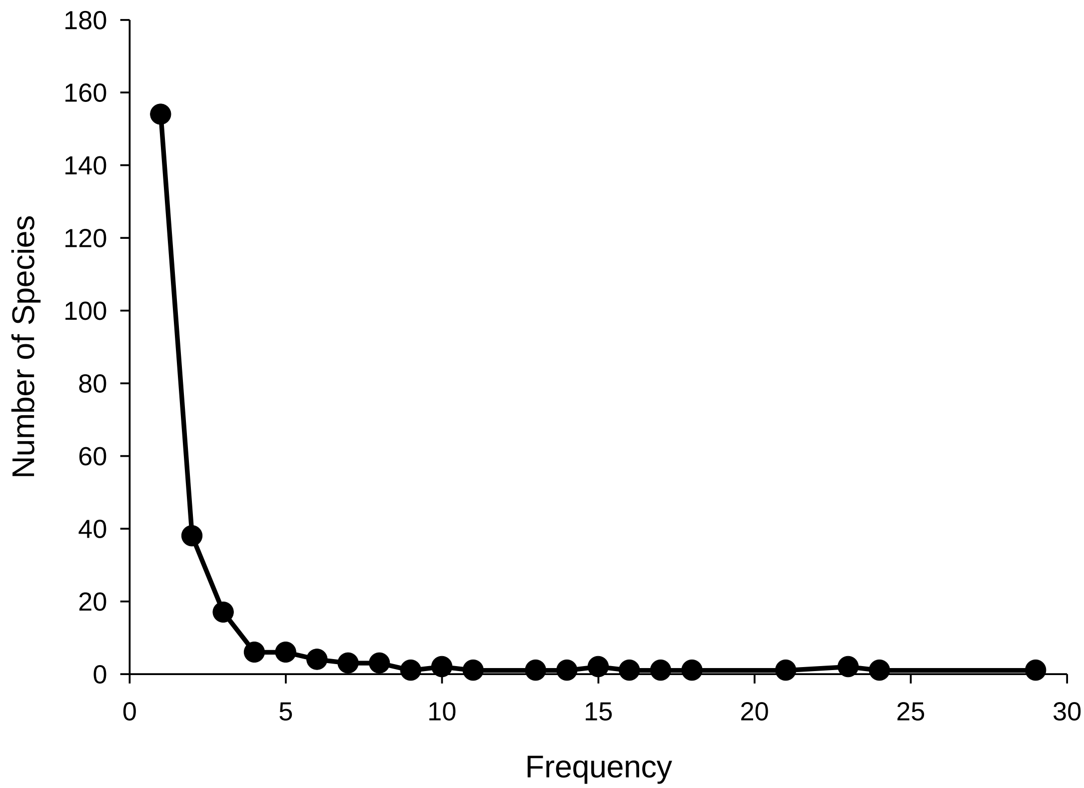

Figure 2.6:The frequency at which each of the 247 nonindigenous species were reported within the 270 research papers reviewed for analysis.

2.5 Discussion

Nearshore development is altering the natural mosaic of habitats in coastal marine systems. These infrastructure changes offer different habitat configurations in novel spatial arrangements for marine species to exploit (Glasby and Connell, 1999; Connell, 2001; Glasby, 2007). A simultaneous expansion of maritime vector activity and introductions of NIS, often directly associated with man-made structures, is playing an increasingly important role in nearshore distributions of populations and communities. This study evaluated the patterns associated with these interacting environmental stressors (habitat alteration and NIS). The literature review revealed that there is a notable interaction between habitat-type and taxa-type in the distribution of NIS.

2.5.1 Habitat utilization by marine invaders

The results show that despite natural habitats being studied more often overall (Figure 2.5), a higher number of NIS were reported from anthropogenic ones (Figure 2.1) but this pattern varied depending on the type of organism(s) studied. Algal and mobile NIS were most often associated with natural habitats while sessile NIS were largely associated with anthropogenic habitats. Structural differences between natural and anthropogenic habitats undoubtedly affect NIS distributions. The most studied algal NIS (*S. muticum*), mobile invertebrate (*H. sanguineus*), and sessile invertebrate (*B. violaceus*) from the literature search help to illustrate this. Each of these NIS is a conspicuous invader of several different bioregions outside their native range, which probably explains the propensity for research on them. *Sargassum muticum* was reported from anthropogenic habitats in five studies and from natural habitats in 20 studies. The growth of algal species can be inhibited by shade (Reed and Foster, 1984; Miller and Etter, 2008), which is a common feature of undersides of floating docks, subtidal pilings, and vertical piers. *Sargassum muticum* does occur in these habitats, but its success as an invader is based on transport via human vectors as well as spread into natural habitats via its inherent dispersal capability (Norton, 1992). Similarly, *H. sanguineus* (mobile) was reported only from natural habitats in 14 different articles. Man-made habitats, like seawalls, tend to have lower numbers of mobile species compared to natural hard benthos because of homogenous surfaces and minimal access to crevices and other micro-habitats (Chapman, 2003). Only mobile NIS that inhabit the fouling matrix present on anthropogenic structures are likely to prosper in such circumstances. In contrast, the 25 studies that documented *B. violaceus* (sessile) from anthropogenic habitats substantially outnumbered the eight articles reporting it from natural habitats. Unlike the case for algae, invertebrate recruitment and space occupancy appears to be promoted by vertical, shaded, over-hanging, floating, and homogeneous surfaces (Young and Chia, 1984, Miller and Etter, 2008; Dafforn et al. 2009), which may help explain the disparity in habitat occurrence records for *B. violaceus*. However, the eight studies that reported its occurrence on rocky benthos (see AppendixA TableA.2 for list) highlight its ability to spread into (infiltrate) natural habitats and communities and suggest that this level of infiltration may be under appreciated.

There is growing evidence that anthropogenic habitats are 'hotspots' for marine invasions (Lambert and Lambert 2003, Glasby et al. 2007; Ruiz et al. 2009, Bulleri and Chapman, 2010), particularly for sessile NIS (this study), but comparatively little is known about whether anthropogenic structures may promote localized dispersal and spread ($10^0 – 10^2$ m) of NIS into adjacent natural habitats. Although many sessile invaders such as sponges, bryozoans, and ascidians have short dispersal distances (meters) because of their limited larval durations (Shanks, 2009), they release very large numbers of propagules and can reach high abundances in anthropogenic habitats (Lambert and Lambert, 2003 Floerl et al. 2009a). As long as larvae are not retained within boundaries of anthropogenic habitats (e.g. Floerl and Inglis, 2003), abundant propagules from dense founder populations should increase the chance of high 'propagule rain' (Lockwood et al. 2009) contributing to initial localized transfer and colonization success. For this to occur, however, hard benthic surfaces need to be available for colonization. In many geographic areas, such as estuaries, where human-vectors of NIS are most active and high numbers of NIS can be found, there is often little natural hard benthic habitat (Ruiz et al. 2009) which may restrict localized dispersal and spread of sessile NIS.

2.5.2 Patterns among habitats and potential sampling biases

The most striking pattern from the literature review was the difference in the types of nonindigenous taxa reported from anthropogenic versus natural habitats. Few reports of algae and mobile NIS came from marina docks, pilings and other man-made structures.

This contrasted with reports of sessile invertebrates, which largely came from anthropogenic habitats. It is difficult to determine to what extent this pattern results from real differences in actual species distributions and how much was due to habitat sampling bias by ecologists (see Ruiz et al. 2000 for a discussion of biases in large-scale geographic patterns of invasions). The analyses do provide some clues, however.

First, studies spanning both anthropogenic and natural habitats were few compared to those that sampled just one or the other (Figure 2.5). This undoubtedly contributed to the high numbers of NIS reported from just one habitat type only. Second, community studies can have an important effect on recorded NIS habitat distributions. For example, a majority of benthic mobile NIS have been recorded in natural habitats only. However, one published study of fouling communities in marinas (Cohen et al. 2005) provided 20 unique records for mobile NIS and a further six that also were reported in other studies, resulting in a contribution of 60% of the records for mobile NIS in anthropogenic habitats. Presumably, additional studies of this nature would increase the records for mobile NIS in anthropogenic habitats and it may be premature to conclude that many mobile species tend not to occur in this habitat type. Third, an uneven taxonomic sampling effort can further bias the overall patterns observed (Ruiz et al. 2000). For example, of the 15 tube-dwelling polychaetes (categorized with sessile species) reported in the literature, a majority were reported from natural habitats alone. However, 75% of the unique records for tubiculous polychaetes in natural habitats were reported by one taxonomist (and colleagues, see Cinar et al. 2006; Cinar, 2006). Again, rather than infer that polychaete NIS predominate in natural habitats and are absent from anthropogenic ones, it is more reasonable to assume that (i) polychaetes are under-studied and under-reported, and (ii) if the one expert publishing research on polychaete NIS had also sampled anthropogenic habitats, different patterns may well have emerged. Fourth, targeted sampling of specific habitats or specific taxa, sometimes at the same time, can also skew patterns. Rapid assessment surveys for NIS, many of which appear in the unpublished ‘grey’ literature, tend to record many species, but often focus only on anthropogenic habitats. The literature search yielded four such studies (Cohen et al. 2005; Arenas et al. 2006; Ashton et al. 2006; Minchin, 2007); all were conducted in anthropogenic habitats (marinas primarily), two targeted a pre-determined list of NIS, and all contributed multiple NIS records (up to 69). This may disproportionally influence reported patterns of NIS distributions among habitats. The literature search did not encompass all reports of NIS and their habitats and this is by no means an exhaustive list of potential sources of bias in our understanding of NIS distributions. However, it does illustrate how our understanding of invasion patterns must also take the research patterns of ecologists into account (Ruiz et al. 2000; Pyšek et al. 2006; Pyšeket al. 2008).

Sessile NIS are a diverse component of epibenthic coastal marine communities throughout the world (Ruiz et al. 2000; Hewitt et al. 2004; Gollasch, 2006). The data show clearly that when NIS sampling occurs in anthropogenic habitats, sessile species are the dominant type of organism recorded. The number of sessile NIS recorded solely from anthropogenic habitats (63) was not substantially higher than reported sessile NIS richness from natural habitats (55). Therefore can we infer that distribution patterns of sessile NIS are well understood in natural and anthropogenic habitats? A comparison of the number of observation records per sessile NIS and across sessile phyla suggests not. More than half of the sessile NIS reported solely from anthropogenic habitats (41 of 63 species) were recorded from only one study (i.e. “singletons”). In fact, the rate of singletons for sessile species reported only from natural habitats (85%) - as well as algae (83%) and mobile (93%) species reported only in anthropogenic habitats - reinforces the idea that occurrence records for a majority of NIS are few.

Furthermore, comparisons across phyla served to reinforce a divide among types of taxa and the habitats from which they are reported. The most studied sessile invertebrate phyla/groups (bryozoans and ascidians) were overwhelmingly reported from anthropogenic habitats (Figure 2.2). In total, 17 (or 56%) of the 30 ascidian NIS were reported solely from anthropogenic habitats, while 12 were reported from artificial and natural habitats and one was reported in natural habitats only. However, 86% of the 197 records for these 30 nonindigenous ascidians came from anthropogenic habitats. In their native ranges, all of these species are found in natural habitats (because their existence pre-dates anthropogenic structure). This begs the question as to whether these NIS are (i) restricted to anthropogenic habitats in their non-native range, (ii) not being reported from natural habitats (non-reporting of zeros), or (iii) simply not being looked for in appropriate natural habitats. Ultimately, the patterns discovered during this study reflect both actual distributions of NIS among habitats, and sampling bias in ecology that can only be resolved using standardized (balanced) sampling protocols across habitats that would allow meaningful comparisons among studies.

2.5.3 Conclusion

It is simplistic to suggest that habitat alone can affect the presence or absence of NIS (Lonsdale, 1999), but it is informative to understand the distribution of species across habitat types, which can inform tests and analyses of other factors which may affect establishment. For instance, characterizing the habitat utilization by *Carcinus maenas*, a nonindigenous crab on the East coast of the U.S., lead to experimental tests which showed that biotic resistance (through predation by a native predator) can limit the abundance and geographic range of an invader (deRivera et al. 2005). In marine systems, a number of factors important to NIS establishment interact with human populations – such as, increased disturbance (Clynick et al. 2009; Bulleri and Chapman, 2010), increased propagule pressure through human-mediated vectors (e.g. commercial shipping) (Verling et al. 2005), and increased availability of resources through the creation of novel man-made habitats.

Anthropogenic habitats play an important role in marine invasions by interacting with vectors and creating conditions that select for different types of species. Results suggest that anthropogenic habitats may be areas of high invasion success, especially for sessile invertebrate invaders. It is important to recognize, however, that observed invasion patterns are ‘apparent patterns’ because there are several sampling biases that ecologists may impose on their data either directly or indirectly (Ruiz et al. 2000; Pyšek et al. 2008; Ruiz et al. 2009). This study highlighted important interactions between patterns of NIS distributions among habitat types. Understanding the habitat distribution of invaders helps us to recognize which invaders and habitat types take priority for conservation. Anthropogenic habitats generally do not hold high conservation value, but further investigation of their role as invasion sites and potential launching points for infiltration of natural habitats will provide insight into the factors affecting establishment and subsequent spread of NIS.

Chapter 3: Anthropogenic habitats and the infiltration of natural benthos by invasive ascidians*

3.1 Abstract

Anthropogenic habitats such as marinas and docks are focal points for sessile marine invasions, but relatively little is known about the infiltration of nearby natural habitats by these invaders. To address infiltration by four geographically widespread ascidian invaders, I used a two-step approach, (i) a field survey with equitable sampling in adjacent anthropogenic and natural habitats in British Columbia, Canada, and (ii) a literature review, to infer larger scale patterns across species' introduced global ranges. Field surveys revealed differential distribution patterns among the four ascidians recorded, with infiltration of natural rocky habitats by two species, *Botrylloides violaceus* and *Botryllus schlosseri*. *Didemnum vexillum* and *Styela clava* were not recorded in natural habitats, though they were both recorded on adjacent artificial structures. Globally, these ascidian species are predominantly found associated with anthropogenic habitats including floating docks, pilings and aquaculture installations, but they have infiltrated natural habitats in some areas of their introduced range. The factors contributing to infiltration of nearby natural benthic habitats remain unclear, but determining which mechanisms are important for encouraging or hindering the establishment and spread of nonindigenous species beyond artificial structures requires survey and experimental work beyond anthropogenic habitats. Such work will aid our understanding of marine introduction dynamics, invasiveness, and associated management implications.

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3.2. Introduction

As the world's human population has grown and coastal development continues apace, there has been a dramatic increase in the amount of artificial structure added to marine environments (Glasby and Connell, 1999; Airoldi et al. 2009; Bulleri and Chapman, 2010).These anthropogenic habitats, such as floating docks, pier pilings, breakwaters, and seawalls, provide novel substrata known to harbor marine communities that differ from surrounding natural substrata (Butler and Connolly, 1996; Glasby, 1999a; Connell, 2000; Chapman, 2003; Bulleri and Chapman, 2004). Specifically, artificial structures are known to be focal points for marine invasions (Lambert and Lambert, 2003; Ruiz et al. 2009) and studies have shown that non-native species are often more prevalent than native species in these man-made environments (Lambert and Lambert, 1998; Glasby et al. 2007; Floerl et al. 2009a). Stepping stone invasions of nonindigenous species (NIS) from one man-made habitat to another via human-mediated vectors are well known (Apte et al. 2000; Floerl et al. 2009b; Goldstein et al. 2010), but much less is known about smaller-scale dynamics between NIS on anthropogenic structures and the infiltration of nearby natural habitats by these species.

Anthropogenic habitats may be particularly susceptible to biological invasions because they are linked to human-mediated vectors of NIS; and as such, are directly supplied with nonindigenous propagules through shipping, recreational boating and aquaculture transfers(Carlton and Geller, 1993; Naylor et al. 2001; Floerl and Inglis, 2005). Further, by facilitating the transport of NIS from one anthropogenic habitat to another, these vectors may select for species that are better adapted to these habitats, such as those that are floating (Glasby et al. 2007; Dafforn et al. 2009) or frequently disturbed (Bulleri and Airoldi, 2005; Piola and Johnston, 2008). Because artificial structures tend to be associated with urban environments and human activity, disturbances from maintenance activities, heavy metals, oil discharges, and anti-fouling paint pollution are more frequent (Turner et al. 1997; Benedetti-Cecchi and Chato Osio, 2007; Piola and Johnston, 2008). Such disturbance can enhance invasion success by periodically removing already established communities and functionally providing ‘new’ substratum for species settlement (Elton 1958; Hobbs and Huenneke, 1992; Lozon and MacIsaac, 1997).

As artificial structures become more ubiquitous in coastal environments, it is important that we understand the link between these ‘hubs’ of marine invasions and areas of natural habitat. The amount of natural benthic hard substratum varies widely among bays and estuaries, but the creation of artificial structures may provide islands of substratum for colonization by arriving propagules. In areas where anthropogenic habitats are limited, but natural hard substrata dominate (e.g. open rocky coasts), far fewer NIS have been recorded on natural substrata than within sheltered estuaries and bays that often have a greater number of man-made habitats and a greater amount of NIS vector activity (Wasson et al. 2005; Preisler et al. 2009; Ruiz et al. 2009). Similarly, within a bay or estuary, sampling of adjacent sites has shown that lower numbers of NIS, particularly sessile species, are found in natural habitats compared to nearby anthropogenic ones (Glasby et al. 2007; Marins et al. 2010). The lack of sessile NIS in natural habitats suggests that many species may be restricted from naturally self-dispersing and recruiting outside of anthropogenic habitats or that natural habitats are in some way resistant or otherwise inhospitable for NIS establishment (e.g. through native community resistance).

Nonindigenous ascidians often dominate the sessile filter-feeding invertebrate fauna found on artificial structures (Lambert and Lambert, 1998; Lambert and Lambert 2003).Some of these species are invasive and have had negative economic (Carver et al. 2003; McKindsey et al. 2007) and ecological impacts (Blum et al. 2007; Lutz-Collins et al. 2009) in receiving ecosystems. Most of these impacts are reported from anthropogenic habitats such as shellfish farms or experimental studies conducted from floating docks. In some cases, however, impacts of nonindigenous ascidians have been documented in natural benthic habitats, including altering community structure through competition with native species for space and resources (Castilla et al. 2004). Here I carried out an *in-situ* field survey and determined the extent to which invasive ascidians have infiltrated adjacent natural rocky benthos. The surveys focused on four nonindigenous ascidians that are known to have been introduced into British Columbia

(BC): *Botrylloides violaceus* Oka, 1927, *Botryllus schlosseri* (Pallas, 1766), *Didemnum vexillum* Kott, 2002, and *Styela clava* (Herdman, 1881). I examined differences in the relative abundance and distribution of these nonindigenous ascidians using equal sampling of artificial structures (marina docks and pilings) and nearby natural rocky reefs. I also assessed community composition of invertebrate and algal taxa between habitat types and locations for comparison with ascidian distributions. Finally, I compared these results to the published literature and inferred larger scale patterns of distributions among habitat types throughout these species' introduced ranges.

3.3Methods

3.3.1 Study species

Three colonial species: *B. violaceus*, *B. schlosseri*, *D. vexillum*, and one solitary species, *S. clava* were targeted. Three of the species, *B. violaceus*, *S. clava* and *D. vexillum* are native to the Northwest Pacific (Cohen, 2005; Stefaniak et al. 2009), whereas *B. schlosseri* is considered a native of European and Mediterranean coastlines (Cohen, 2005). These four species are geographically widespread marine invaders, being introduced to multiple locations in temperate regions around the world (Lambert and Lambert, 1998; Lambert and Lambert, 2003; Lambert, 2009; Goldstien et al. 2011). All four species are known to affect shellfish aquaculture, particularly in Eastern North America, and are therefore considered invasive in a number of areas where they have been introduced (McKindsey et al. 2007; Lambert, 2009). They are readily identifiable in the field and their distribution in natural rocky habitats in southern B.C. was unknown prior to this study (Gartner, 2010). *Didemnum vexillum* was previously collected from three subtidal benthic rock sites in British Columbia (see Bullard et al. 2007), but this study did not provide any details on its abundance or distribution at these sites. All four species are believed to have been introduced to B.C. relatively recently, with all being first reported within the last 20 years: *B. violaceus* in 1992 (Cohen, 2005), *B. schlosseri* in 1998 (Cohen, 2005), *D. vexillum* in 2003 (Lambert, 2009) and *S. clava* in 1993 (Lambert, 2003).

3.3.2 Field Survey

Surveys were conducted using SCUBA at eight locations along approximately 115km of south-eastern Vancouver Island, British Columbia, Canada (Table 3.1) in July-August 2008 (with one exception – Silva Bay was surveyed in July 2009). Each location consisted of a marina and adjacent natural rocky reef and sampling was carried out on dock floats, marina pilings, and natural rocky reefs. All of the dock floats were made of Styrofoam and the pilings were creosote-treated wood, except for Nanoose Bay, which had polyethylene-plastic floats and steel pilings. The natural rocky reefs were within 150 m of each marina and included areas of subtidal bedrock with boulder/rocky scree mixed with intermittent sandy patches. All three habitat types were sampled in each location on the same or consecutive days.

Table 3.1:Location and sampling date information for each of the locations surveyed. At each location both the marina and the adjacent subtidal rock were sampled.

Location	Latitude	Longitude	Sampling Date
Nanoose	49°17'13" N	124°08'06" W	22/07/2008
Silva Bay	49°08'58" N	123°41'52" W	14/07/2009
Thetis Island	48°58'67" N	123°40'15" W	13/11/2008
Maple Bay	48°47'45" N	123°36'08" W	23/07/2008
Patricia Bay	48°39'90" N	123°26'58" W	09/07/2008
Cadboro Bay	48°27'04" N	123°17'42" W	07/07/2008
Oak Bay	48°25'29" N	123°18'56" W	21/08/2008
Victoria Harbour	48°25'42" N	123°23'40" W	19/08/2008

To survey dock floats and rocky reefs, eight random 2×5 m areas were delineated underwater using measuring tapes (for a total 80 m^2 per habitat type). Eight pilings were also surveyed per marina, however, the total area surveyed varied by depth and piling circumference. The depth of the pilings was never greater than 5 m below mean low water springs (MLWS) and was recorded by a Suunto Dive Computer. Within each of the eight areas in each habitat type, one diver identified and counted all individuals (for solitary species) or individual colonies (for colonial species) of the nonindigenous ascidians present. The second diver took five haphazardly placed photographs using a digital camera attached to a 30×30 cm PVC quadrat frame (40 photo-quadrats per habitat type, per location). On dock floats, species counts and photographs were made on the horizontal underside of the floating pontoons. On the pilings, sampling was carried out at varying depths below MLWS in an effort to accurately characterize ascidian densities within subtidal portions of the vertical pilings. For rocky reefs, vertical rock surfaces from 1-5 m below MLWS, including bedrock and boulders, were targeted to standardize the orientation and depth of substratum. In addition, a 20 minute survey swim (by two divers, 40 minutes total) of the rocky reef was carried out to look for the presence of nonindigenous ascidians that may have been missed within the eight survey areas.

3.3.3 Analysis of Field Survey Data

Mann-Whitney *U* tests (for two groups) and Kruskal-Wallis tests (for three groups)were used to look for significant differences in the median densities of ascidians within habitat types and locations (using MINITAB 15). Multivariate analyses of photo-quadrat data (Version 5PRIMER-E Ltd, Plymouth) were used to assess community composition and the role of nonindigenous ascidian distributions in community dissimilarity among locations and habitat types. A sub-sample of nine digital photographs from each of three habitat types per location were randomly selected and analyzed for percent cover of taxonomic groups (see Table 3.2) and bare space (27 photo-quadrats per habitat per location). Percent cover was quantified by superimposing a 100 point grid onto each photograph and counting the taxa occurring under each point (using IMAGEJ 1.41, National Institutes of Health, USA). In cases where one organism was overgrowing another, only the organism on top was recorded. Digital photographs of sufficient quality were unavailable for Oak Bay and Victoria Harbor so community analyses were confined to the remaining six locations. Non-metric multidimensional scaling (nMDS), based on a square-root transformed Bray-Curtis similarity matrix, was used to assess community patterns and distinctness of assemblages between locations and habitat types. Differences in the composition of taxonomic groups between habitats nested within locations were tested using a two-way analysis of similarity (ANOSIM). A similarity percentages analysis (SIMPER) was used to identify which taxonomic groups contributed most to the dissimilarity between anthropogenic and natural habitat types.

Table 3.2: The twenty-five taxonomic groups used throughout community analyses. Digital photographs were analyzed in ImageJ 1.41 (U.S. National Institutes of Health, Bethesda, MD, USA) for percent cover of taxonomic groups using a 100-point overlay grid.

Taxonomic Grouping
Algae-Brown
Algae-Green
Algae-Red
Amphipod
Anemone
Ascidian-Native Colonial
Ascidian-Native Social
Ascidian-Native Solitary
Ascidian-Non-indigenous Colonial
Ascidian-Non-indigenous Solitary
Asteroid
Barnacle
Bivalve
Bryozoan-Encrusting
Byrozoan-Branching
Chiton
Decapod
Echinoid
Gastropod
Holothurian
Hydroid
Isopod
Nudibranch
Polychaete
Sponge

3.3.4 Literature Review

To investigate the documented distribution of the four target species in anthropogenic and natural habitats throughout their native and introduced range, I surveyed the published literature from 1955-2010 using the ISI Web of Science search engine (Thomson Reuters Web of Science-accessed April 2011). I used the 'topic' search function to search for the target species in the titles, abstracts and keywords of published papers. For each species I searched for the species name and the names of synonymized taxa as listed in the Ascidia World Database (Shenkar et al. 2011). Since the identity of *D. vexillum* only recently has been determined (see Lambert 2009; Stefaniak et al. 2009) I searched for both *Didemnum* sp. and *D. vexillum*. One marine invasions journal, *Aquatic Invasions*, was not adequately covered by Web of Science and was therefore searched directly via its website.

Only those studies that provided a detailed description of where a species was reported or collected were included in analyses. I searched through the body of each paper to determine the type(s) of habitat and geographical location for each species record. I recorded habitat details, including whether it was subtidal or intertidal, floating or fixed and what type of substratum it was. Habitat data were used to compare the frequency of species occurrence in anthropogenic and natural habitats (Chi-square tests). Anthropogenic habitats included dock floats, pilings, aquaculture installations, artificial rock (e.g. rip-rap or breakwaters) and piers. If a sampling apparatus (such as PVC tiles) was hung from one of these structures, it was categorized with the structure the apparatus was hanging from. Natural habitat included intertidal and subtidal bedrock, cobble and boulder substratum, and biogenic habitats such as algal fronds and natural oyster beds. Occurrence records were divided into 17 geographic areas based on locations mentioned in the reviewed literature and marine ecoregions of the world (Spalding et al. 2007). The corresponding marine ecoregion(s) from Spalding et al. (2007) are noted in parentheses after each geographical area. The 17 areas were a) Alaska (55),b) British Columbia, Washington and Oregon (56, 57),c) Northern California (58), d) Southern California (59),e) Eastern Canada (37, 38, 39), f) New England (40), g) Virginia (41), h) South America – Chile, Argentina (184, 187),i) British Isles (26), j) North Sea – Holland, Germany, Denmark (25),k) Atlantic Europe –France, Spain, Portugal (27),l) Western Mediterranean, (35), m) Eastern Mediterranean (32), n) Japan (48, 49), o) China – Yellow Sea (50), p) Southeastern Australia (203), and q) New Zealand (196, 199, 200).Within each area, I determined whether a species had been reported from anthropogenic, natural, or both types of habitats. The data represent the best available records of species distributions using a systematic literature survey, but do not include grey literature (e.g. agency reports, internet articles or theses).

3.4. Results

3.4.1 Field Survey

All four targeted nonindigenous ascidians were observed during the field surveys. *B. violaceus* was the most abundant, reaching the highest densities recorded and occurring most frequently among sites (seven of eight locations surveyed; Figure 3.1). *Botryllus schlosseri* was found at four locations, *S. clava* at three, and *D. vexillum* at just one. *B. violaceus*, *B. schlosseri* and *S. clava* were recorded more frequently on dock floats compared to pilings and natural rocky reefs. For all four species, the density of ascidians was always greater on dock floats or not significantly different between floats and pilings (see Mann-Whitney *U* tests Table 3.3). Only two of the four species were detected on adjacent rocky reefs. *Botrylloides violaceus* was recorded on natural habitat at three locations and *B. schlosseri* at two (Figure 1). The density of these species on rocky reefs did not differ significantly from densities on anthropogenic substrata in all but one instance: the density of *B. violaceus* on rocky reefs at Thetis Island was significantly lower than the density on marina floats(H_2 = 9.53, d.f.=2, $P < 0.01$).

The composition of invertebrate and algal assemblages did not differ significantly among locations across the study region (ANOSIM, Global R: -0.055, P= 0.632; Figure 3.2a). However, there was a significant effect of habitat type on assemblage composition (ANOSIM, Global R: 836, P<.001; Figure 3.2a). The percent cover of nonindigenous ascidians contributed to this trend, with nonindigenous ascidians being more abundant on floats and pilings (Figure 3.2b). SIMPER analysis revealed that pair-wise habitat dissimilarity was greatest between floats and rocky reefs (97%), followed by pilings and rocky reefs (94%) and floats and pilings (84%). SIMPER analysis also showed that bivalves, anemones, and bryozoans were characteristic of anthropogenic habitats whereas algae were far more prevalent on rocky reefs than floats and pilings. These sets of taxa contributed most to differences between anthropogenic and natural habitats (Table 3.2).

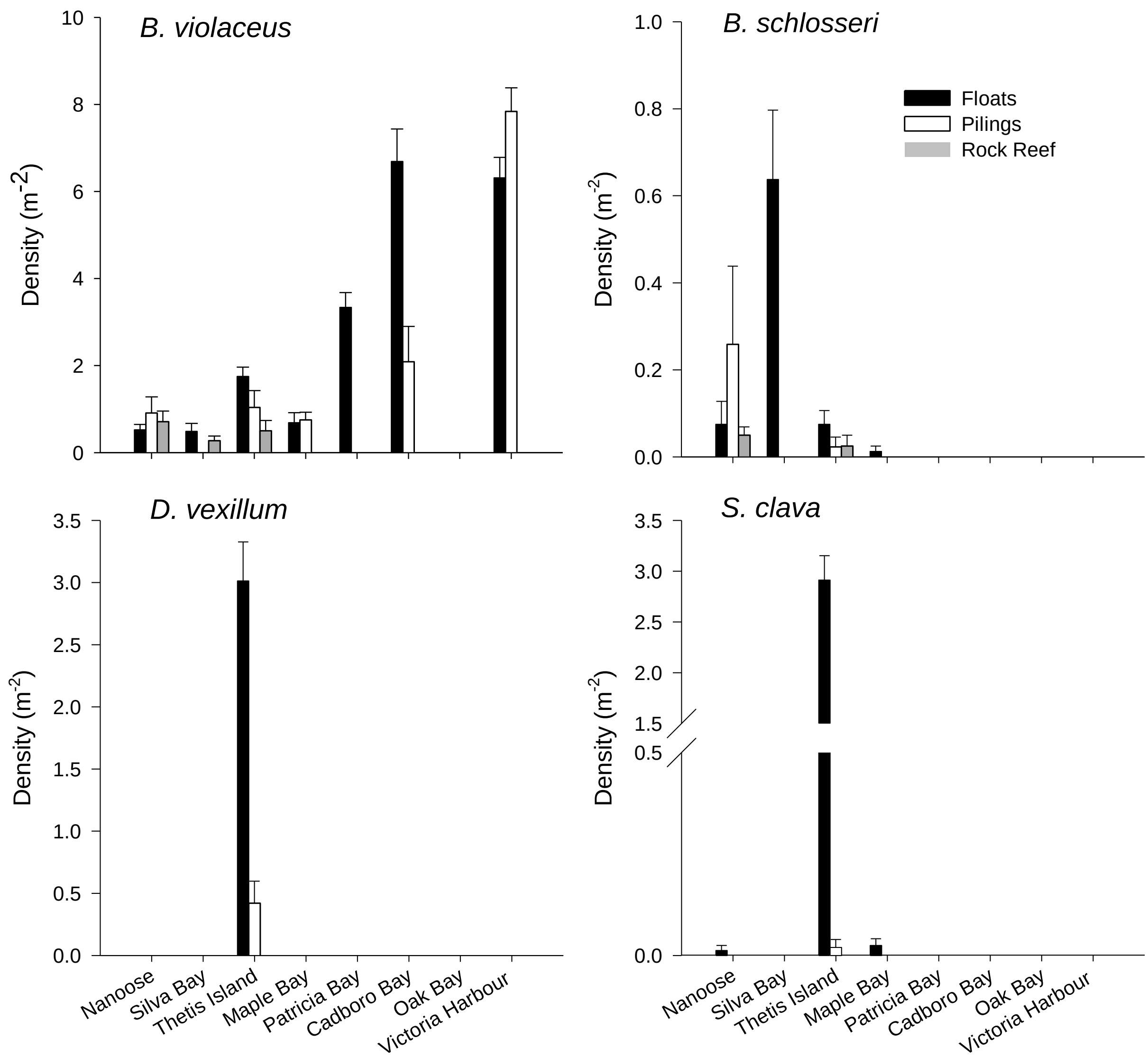

Figure 3.1:Ascidian densities across locations and habitats. The mean density (m^{-2}) and standard error of *Botrylloides violaceus* Oka, 1927, *Botryllus schlosseri* (Pallas,1766), *Didemnum vexillum* Kott, 2002, and *Styela clava* (Herdman, 1881)is shown for each habitat type (dock floats, pilings or rocky reef) per location (listed from north to south).

Table 3.3: Mann-Whitney *U* tests comparing the density of ascidians on the two anthropogenic habitats surveyed (i.e. dock floats and pilings).

	Botrylloides violaceus		*Botryllus schlosseri*		*Didemnum vexillum*		*Styela Clava*	
	W	P-value	W	P-value	W	P-value	W	P-value
Nanoose	51	0.076	66	0.836	Not Found		Floats Only	
	Floats = Pilings		Floats = Pilings					
Silva Bay	Floats Only		Floats Only		Not Found		Not Found	
Thetis Island	90	0.024	88	0.141	100	0.001	100	0.001
	Floats > Pilings		Floats = Pilings		Floats > Pilings		Floats > Pilings	
Maple Bay	62.5	0.597	Floats Only		Not Found		Floats Only	
	Floats = Pilings							
Patricia Bay	Floats Only		Not Found		Not Found		Not Found	
Cadboro Bay	97	0.003	Not Found		Not Found		Not Found	
	Floats > Pilings							
Oak Bay	Not Found		Not Found		Not Found		Not Found	
Victoria Harbor	51	0.083	Not Found		Not Found		Not Found	
	Floats = Pilings							

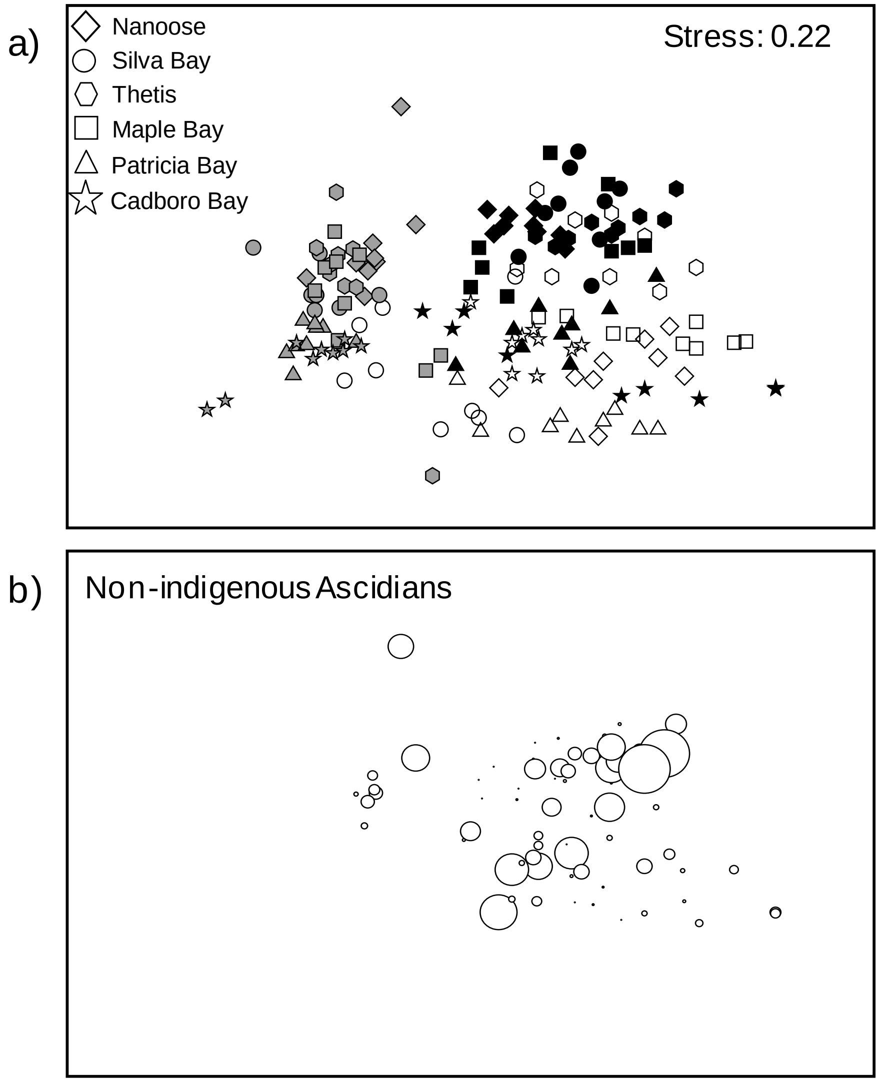

Figure 3.2: Community structure among locations and habitats. A non-metric multidimensional scaling (nMDS) plot of samples from locations and habitats (a) shows clustering by habitat type only, with no significant differentiation of communities among sites. Symbol shapes refer to different locations (see key) and symbol color represents different habitat types for dock floats (black), pilings (white), and rocky reef (gray). The bubble plot (b) uses the same data points but represents the percent cover of nonindigenous ascidians overlaid on the nMDS pattern. It reveals that ascidians were absent or at low densities in rocky reef habitats, but more widespread and abundant in anthropogenic habitats.

Table 3.4: Results of SIMPER analysis showing the five most dissimilar taxonomic groups between each pair of habitats. The habitat type in parentheses indicates which habitat the taxonomic group is characteristic of.

Sites	Taxonomic Groups	Average Dissimilarity	Cumulative % Contribution
Floats vs. Rocky Reef Average Dissimilarity 97.01	Bivalves (floats)	17.40	17.93
	Green Algae (rocky reef)	13.16	31.50
	Anenomes (floats)	10.79	42.63
	Branching Bryozoans (floats)	10.65	53.61
	Brown Algae (rocky reef)	9.47	63.28
Pilings vs. Rocky Reef Average Dissimilarity 94.26	Green Algae (rocky reef)	14.09	14.95
	Branching Bryozoans (pilings)	12.89	28.63
	Encrusting Bryozoans (pilings)	11.36	40.68
	Barnacles (pilings)	10.25	51.55
	Brown Algae (rocky reef)	9.80	61.95
Floats vs.Pilings Average Dissimilarity 83.61	Bivalves (floats)	14.93	17.86
	Branching Bryozoans (floats)	14.26	34.92
	Anenomes (floats)	10.63	47.63
	Encrusting Bryozoans (pilings)	9.03	58.42
	Barnacles (pilings)	7.25	67.09

3.4.2 Literature Survey

The initial literature search returned 666 papers, of which108 referred to the habitat distributions of one or more of the four ascidians throughout the world. Compiling these 108 papers we find that, globally, *B. violaceus*, *B. schlosseri*, *D. vexillum,* and *S. clava* have been reported significantly more often from anthropogenic habitats than natural ones (Figure 3: *B. violaceus*χ^2_1= 18.29, p < 0.0001; *B. schlosseri*χ^2_1= 18.29, p < 0.0001; *D. vexillum*χ^2_1= 8.02, p < 0.0001; *S. clava*χ^2_1= 23.11, p < 0.0001). Over 77% of published reports of these species have come from anthropogenic habitats, with occurrences from dock floats representing the greatest proportion of these records (Figure 3.3). The two botryllid ascidians, *B. violaceus* and *B. schlosseri*, were reported from anthropogenic habitats four times more often than from natural habitats. *Styela clava* was reported five times more often in anthropogenic habitats and *D. vexillum* was reported twice as often (Figure 3). Despite the preponderance of records from anthropogenic habitats, all four species have also been reported in natural hard substrata somewhere throughout their introduced ranges, including subtidal rock or as epifauna on biogenic structures such as algal fronds (Figure 3.4). For example, *D. vexillum* has been reported from natural habitats, such as subtidal bedrock and boulder/cobble/rock, in five of the eight areas where it has been introduced (Figure 3.4). It was not reported from natural habitats in Southern California, Eastern Canada or the British Isles. Throughout their global introduced range, the other three species are largely known from artificial habitats. *Botrylloides violaceus* has been reported from natural habitats in three of the ten geographical areas where it has been introduced; *B. schlosseri* from three of the nine areas it has been introduced and *S. clava* from four of the eleven areas it has been introduced.

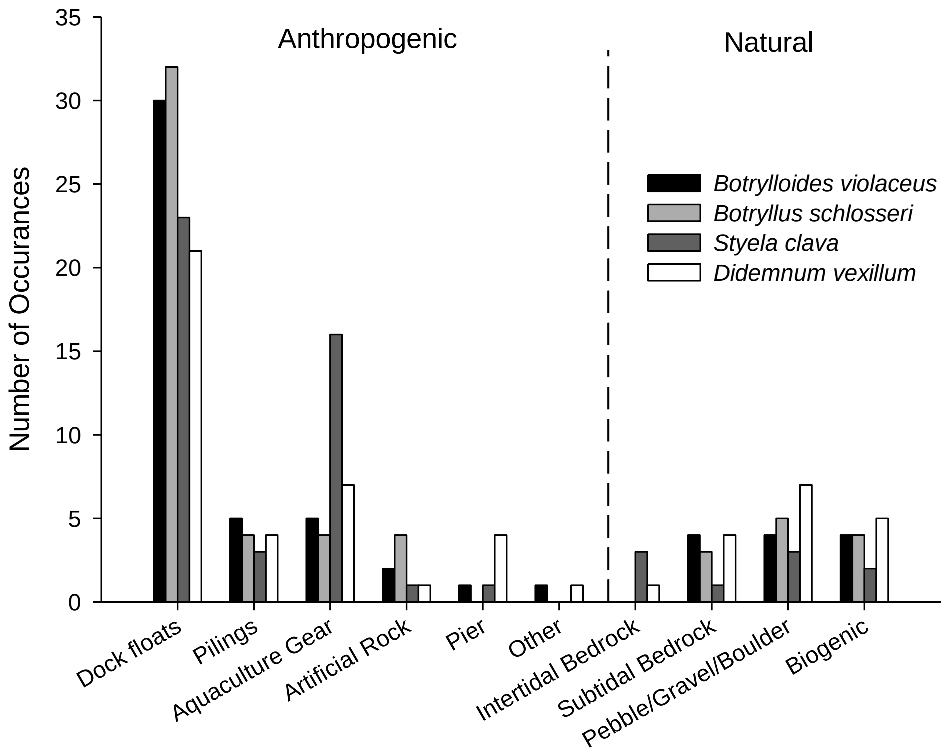

Figure 3.3:The type of habitat(s) where the four nonindigenous ascidian species were reported from the published literature (N=108 total studies). Totals do not sum to 108 because some papers reported multiple species, or reported a species in multiple types of habitats.

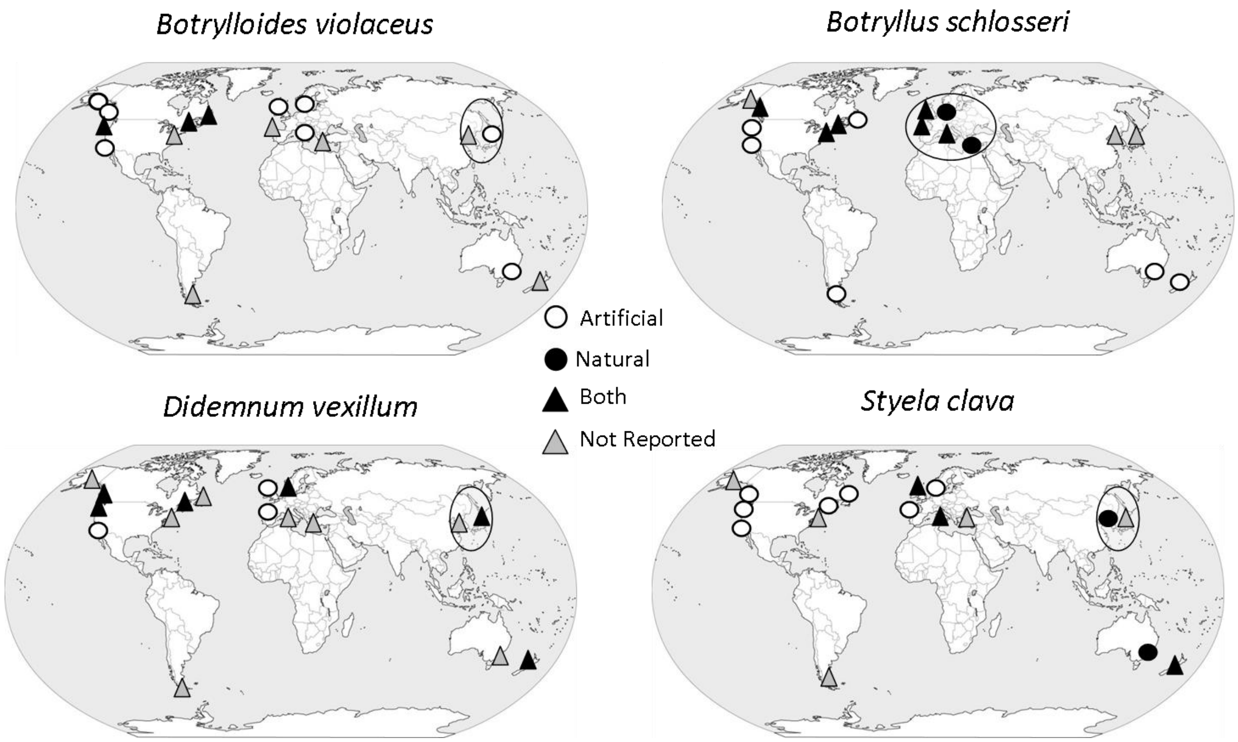

Figure 3.4:Global distribution of the four invasive ascidians and whether they have been reported from anthropogenic or natural habitats. Occurrence locations where divided into 17 geographic areas based on locations mentioned in the reviewed literature and marine ecoregions of the world (Spalding et al. 2007). Symbol color/shape indicates that the published records from an area document the ascidian species in anthropogenic habitats only, natural habitats only, both anthropogenic and natural habitats or that there are no reports from that area (see key). There are 17 symbols per plot and the large ovals represent the native range of each species.

3.5 Discussion

Infiltration of natural habitats and communities by populations of NIS is a fundamental component of invasiveness (Richardson et al. 2000) and is sometimes considered a definitional difference between an 'introduced' species and an 'invasive' one (Colautti and MacIssac, 2004). In coastal marine systems, sessile invertebrates are a significant component of nonindigenous assemblages (Byrnes et al. 2007), but the degree to which they have infiltrated natural habitats is not well understood for most species in most locations. In contrast, the role of anthropogenic habitats as hubs of NIS is well documented (Chapman and Carlton, 1991; Lambert and Lambert, 2003; Arenas et al. 2006; Ruiz et al. 2009). It is also known that different sampling strategies can strongly bias the interpretation of results. Thus, deciphering the extent to which limited distributions of sessile invaders in natural benthos is a function of individual investigators prioritizing anthropogenic habitats for sampling or a real pattern of limited infiltration is essential to better understanding invasion dynamics.

The prevalence of *B. violaceus*, *B. schlosseri*, *D. vexillum* and *S. clava*in anthropogenic habitats, both locally (in B.C.) and globally, adds to the array of records linking marine invasions and artificial structures. I recorded only one un-invaded anthropogenic habitat (a marina) among the eight that were surveyed for ascidians throughout southeastern Vancouver Island. In addition, by carrying out *in-situ* surveys with equal sampling across both anthropogenic and natural habitats, I was able to record the differential infiltration patterns of these four nonindigenous ascidians. While it appears that artificial structures are integral to sessile invader establishment, and that subsequent spread to other anthropogenic habitats is commonplace (Rius et al. 2008; Darling et al. 2009; Bock et al. 2010), the rate of 'escape' from anthropogenic habitats and processes underlying successful infiltration remain less well understood. A handful of studies have examined invader distribution patterns between artificial structures and the surrounding natural rocky substrata (see Lambert, 2002; Page et al. 2006; Glasby et al. 2007; Shenkar and Loya, 2008; Marins et al. 2010). Although these studies targeted different geographic locations and species, all revealed greater NIS abundance in anthropogenic habitats. As areas of high NIS abundance, anthropogenic habitats may act as reservoirs for the subsequent spread and infiltration of nearby marine benthos. However, knowledge of their spread or 'release' from artificial structures to nearby natural habitats is limited. The underlying mechanisms influencing the connection between anthropogenic and natural habitats is even less well known.

Botrylloides violaceus was by far the most abundant ascidian encountered in this study. It was present at seven of eight locations, and in Victoria Harbor reached abundances of up to nine colonies m^{-2} in anthropogenic habitats. Comparable sampling of natural rocky reefs revealed that *B. violaceus* has also successfully infiltrated natural habitats, but currently occurs at low densities (< 1 colony m^{-2}) and at only three of seven locations where it was recorded on adjacent artificial structures. Although seemingly counter-intuitive, the results suggest that high densities in anthropogenic habitats do not necessarily contribute to successful infiltration of adjacent rocky reefs. Occurrences in adjacent natural habitats did not coincide spatially with the marinas of highest *B. violaceus* density. Among the other three species targeted in the field survey, only *B. schlosseri* was recorded in natural rocky habitats. It was found in two of eight rocky reefs surveyed, but always in low abundance (< 0.1 m^{-2}). Although I did not find *D. vexillum* or *S. clava* on any of the reefs that were surveyed, the literature review showed that all four species have been reported from natural habitats within their introduced range (Figures 3.3 and3.4). This suggests that these species do have the ability to infiltrate and establish in natural benthic habitats, which is not surprising given that they inhabit natural benthos in their native range (Figure 3.4). Nevertheless, in southern B.C. and in parts of their introduced range, it appears as though some combination of factors is reducing their success in natural benthos. One possibility may simply be a lack of sampling for nonindigenous ascidians in natural benthos in non-native ranges. However, taken together, field results and inferences from the literature suggest that infiltration of natural habitats is often limited and that several factors, hypothesized below, may contribute to these realized distributions.

A primary factor is the proximity to suitable natural habitat in relation to the dispersal capacity of the species. Lockwood et al (2009) used the term 'propagule rain' to describe localized propagule pressure that enables NIS to spread from initial points of establishment. Limitations on the successful dispersal of propagules may be especially relevant to sessile marine invertebrates that are restricted to benthic hard substrata and often lack long dispersal capabilities (Butler and Keough, 1990; Shanks 2009). In this study, to reduce the likelihood of dispersal limiting the distributions of species, I sampled the nearest rocky reefs, most of which were within 150m of the adjacent marina. Of course, for many subtidal marine ecosystems (bays and estuaries in particular), nearby natural hard substratum can be minimal or absent(Connell and Keough, 1985). Artificial structures can act as islands of suitable habitat in this context, so establishment within many estuaries by ascidians and other sessile invertebrates may only be possible on man-made structures. Natural subtidal rock is abundant within the study system, however, and the infiltration of rocky reefs by two species at some locations suggests this might not be a limiting factor in this system.

A number of taxa were recorded on natural rocky reefs, including solitary and colonial ascidians, bryozoans, and sponges, indicating that they were suitable for colonization by sessile invertebrates. Nonetheless, the percent cover of invertebrates, and nonindigenous ascidians, was lower on reefs than on both floats and pilings. The differences in community composition of taxa between anthropogenic and natural subtidal habitat types, regardless of whether a species is native or non-native, is well documented (Glasby, 1999a; Connell, 2000; Chapman, 2003; Bulleri and Chapman, 2004). A number of factors can affect the types of species encountered in each habitat type, including orientation, composition, and substratum heterogeneity(Glasby and Connell, 2001; Chapman, 2003; Glasby et al. 2007), light availability (Glasby, 1999b; Blocky and Chapman, 2006), sedimentation (Airoldi, 2003), exposure (Bulleri and Airoldi, 2005), propagule supply (Svane and Young, 1989; Shanks 2009), competition (Stachowicz and Byrnes, 2006), and predation (Osman and Whitlatch, 1995a; 2004). Determining which factors are responsible for the patterns observed during this study will require further investigation and experimental manipulation. Sedimentation appeared higher in the natural rocky reefs surveyed, but the presence of other sessile invertebrates and algae in these environments suggests that this factor might not limit settlement or survival. Recent laboratory research has shown that all four of the nonindigenous ascidians are susceptible to predation by native benthic species (Epelbaum et al. 2009c). Native predators may be reducing the likelihood of successful infiltration by these ascidian species, but this would need to be tested in the field. Interestingly, when *B. violaceus* and *B. schlosseri* were recorded on rocky reefs in the fieldsurveys, they often occurred as epibionts on algae, particularly on the fronds of non-native *Sargassum muticum*. Their ability to utilize secondary substrata as habitat, such as algal fronds, may help facilitate their infiltration into natural benthos (White and Orr, 2011).

Similar trends have been noted elsewhere for nonindigenous ascidians. A biodiversity survey in Guam reported 15 nonindigenous ascidians from anthropogenic habitats while only three occurred on nearby rocky reefs (Lambert, 2002). Similarly, three nonindigenous ascidian species present on artificial substrata (dock floats and a pier) in a port system in south-eastern Brazil were not present on nearby natural rock (Marins et al. 2010).*Didemnum vexillum* is a particularly good counter-example of a successful infiltrator of natural habitat that can overgrow native species and become locally abundant (Valentine et al. 2007). Although not found on natural habitat during the field survey, *D. vexillum* was reported previously from natural habitats in B.C. (Bullard et al. 2007) and is widely reported from subtidal gravel and rock on the eastern coast of North America, including a 230km^2 area of Georges Bank (Bullard et al. 2007; Valentine et al. 2007) and in New Zealand (Coutts and Forrest, 2007). Other nonindigenous ascidians (*Pyura praeputialis* in Chile for example; Castilla et al. 2004) can reach high densities in natural habitats, but these examples appear to be the exception rather than the rule (Lambert, 2002; Lambert and Lambert 2003; Marins et al. 2010; Figure 3.4).

The results further illustrate the link between human-mediated transport (such as shipping and recreational boating) and anthropogenic habitats in the spread and distribution of marine NIS. For instance, in the 45 years since *B. violaceus* was first recorded on the west coast of North America (in Santa Barbara in 1966; Ruiz et al. 2011), its known invasive range now extends south to Ensenada, Mexico and north to Southeastern Alaska (Lambert and Sanaymyan 2001). Importantly, it is reported primarily from anthropogenic habitats within this range. The larvae of *B. violaceus* remain planktonic for only minutes to hours, suggesting that natural long-distance dispersal over short time-periods is unlikely (Lambert, 2005). Recent genetic analysis supports this hypothesis, suggesting that recreational boating and aquaculture transfers may be key anthropogenic dispersal mechanisms in this region (Bock et al. 2011).As such, *B. violaceus* on the Pacific Coast highlights an important distinction in the invasion ecology of sessile marine species: (i) spread events that appear to occur primarily among anthropogenic habitats over scales greater than kilometers and which are predominantly used to describe geographic range expansion, and (ii) spread over localized scales (10^0 – 10^2 m) referring to the infiltration of natural habitats.

Determining which mechanism(s) are important for encouraging or hindering the establishment and spread of NIS beyond anthropogenic structures will require survey and experimental work outside of these habitats. Much of what is known about subtidal sessile communities, and many of the experimental manipulations of ecological processes in this system, come from research conducted in anthropogenic habitats (see Glasby and Connell, 2001 for review). For example, experimental studies have shown that colonial ascidians are strong spatial competitors (Grosberg, 1981; Russ, 1982; Nandakumar et al. 1993; Osman and Whitlatch, 1995b), suggesting that if their larvae do disperse and settle in natural subtidal hard substrata, they may outcompete native species. However, all of these studies were restricted to anthropogenic habitats (e.g. floating docks, piers, and rafts), which may give ascidians, which are known to be highly abundant on artificial structures, a competitive advantage that may not be evident in natural environments. A similar approach of using experimental apparatus hanging from floating docks has been used to study native community resistance to sessile NIS (Stachowicz et al. 1999; Stachowicz et al. 2002) and invader recruitment under disturbance regimes (Altman and Whitlatch, 2006). It would be instructive to re-examine these results using subtidal benthic communities found on natural substrata in rocky reefs, or to experimentally introduce NIS propagules to rocky reef communities to assess their fate (similar to experiments conducted by Clark and Johnston, 2005, 2009, 2010, but in a natural setting).

3.5.1 Conclusions

The field study revealed differential distribution patterns of four nonindigenous ascidians in B.C. and infiltration of natural habitats by two species. The next step is to determine the role of each factor in creating these patterns. This is the first study to systematically sample natural rocky reefs in B.C. for the presence of sessile nonindigenous species, and insufficient sampling effort of natural habitats in this region, and others, may be a cause of under-reporting infiltration by NIS. Sessile NIS may also occur in such low abundances in natural habitats as to evade detection, ultimately going unreported. Additional surveys would be useful to detect the prevalence of infiltration by these species in other natural sites throughout B.C. and beyond. The results also demonstrate that *in situ* subtidal sampling is required for a better understanding of subtidal NIS distributions.

As coastal environments become more urbanized, artificial structures will continue to be added to the marine environment (Bulleri and Chapman, 2010). Existing patterns of nonindigenous ascidian distributions suggest they thrive in these novel habitats and have the ability to infiltrate natural habitats in some cases. A classic analogy in terrestrial systems is the infiltration of 'garden escapes' into surrounding natural habitats whereby species introduced intentionally for their aesthetic qualities disperse into surrounding native habitats (Reichard and White, 2001; Hulme, 2011). Such escapees have affected the structure, composition, and functioning of ecosystems (Milton et al. 2007; Hladyz et al. 2011). Determining which mechanisms and species characteristics are important for encouraging or hindering the establishment and spread of marine sessile NIS beyond anthropogenic habitats is essential for understanding marine introduction dynamics, invasiveness, and associated conservation impacts – after all, while anthropogenic structures make for convenient platforms to sample and experiment with marine species, the structures themselves are not often considered important habitats for conservation purposes.

Chapter 4: Supply-side invasion ecology: investigating how propagule number and post-settlement survival influence the establishment of the invasive ascidian *Botrylloides violaceus*.

4.1 Abstract

Understanding which factors affect invasion success is a primary goal of invasion ecology. Propagule pressure, or the number and frequency of individuals supplied to a new region, is believed to play a critical role in determining the successful establishment of nonindigenous species (NIS). For many marine species, the period between propagule (or larval) release and recruitment to adult populations is also an important determinant of success, especially for sessile invertebrates. To examine how propagule number and post-settlement stressors interact to affect establishment success I conducted a set of experimental field studies using the invasive ascidian *Botrylloides violaceus*. I manipulated propagule supply in the field and investigated how habitat type, community type, and propagule number affected recruitment. I also followed newly settled *B. violaceus* colonies in the field and assessed how settlement density and access by predators affected survival over time. *In-situ* larval dosing was successful, but after eight weeks there were no differences in recruitment across larval dosing or community type treatments. There were significant differences between habitats, however, with much lower recruitment to fixed tiles (in benthic rocky habitat) than floating tiles (on marina dock floats). Post-settlement mortality in *B. violaceus* was high and access by predators was a significant factor affecting survival. Testing these relationships provided critical insights into factors that influence establishment success and spread, which is essential for predicting and better managing invasions.

4.2 Introduction

The rate of biological invasions continues to increase in modern times as trade and globalization expand (Levine and D'Antonio, 2003; Semmens et al. 2004). Biological invasions are a multi-step process and in order for a species to successfully invade a new region it must survive through a number of successive stages, including transport, introduction, establishment and spread(Blackburn et al. 2011). Understanding which factors affect invasion success through each stage, and to what extent, is a primary goal of invasion ecology (Lockwood et al. 2007; Davis 2009). Recent syntheses across invasion studies suggests that propagule pressure, or the supply of larvae, seeds, or adults plays an important role in the successful establishment of nonindigenous species (NIS) (Kolar and Lodge, 2001; Lockwood et al. 2005, 2007; Colautti et al. 2006; Simberloff 2009). In some cases, the magnitude and frequency of propagule delivery can have a greater influence on establishment success than other biological or environmental factors (Kolar and Lodge, 2002; Lockwood et al.2005; Daehler, 2006). However, propagule pressure likely interacts with other important ecological factors such as the amount of available resources and suitable habitat, levels of disturbance, and the presence of predators or herbivores, to determine the likelihood of successful invasion (Colautti et al. 2006).

The study of propagule pressure is similar to research in supply-side ecology, in that both recognize the role that variable larval (or propagule) input can play in determining the size of local adult populations (Connell 1985; Lewin 1986; Hughes et al. 2000; Johnston et al. 2009). Many marine species are sessile and space-limited as adults, but have an early larval life history stage which is critical to dispersal. Although transport mechanisms differ among species which spread through natural means and those that are anthropogenically introduced to a region, the ecological processes acting on propagules during and after settlement are the same. Once viable propagules are released into a new environment, newly settled larvae must survive post-settlement processes to recruit into the adult population. Biotic and physical factors such as habitat type, the amount of available resources, and the presence of predators in the receiving community can be crucial for determining the size of recruiting populations (Grosberg 1981; Hunt and Scheibling, 1997).

Post-settlement mortality in sessile benthic marine invertebrates can be very high and undoubtedly leads to invasion failure. Data suggests that in most cases over 90% of newly settled individuals do not survive to adulthood, and in studies where data were collected immediately after settlement, mortality in the first two days was often greater than 30% (reviewed by Gosselin and Qian, 1997). For example, in a study of the colonial ascidian *Podoclavella moluccensis*, Davis (1987) found that 63% of settling larvae survived one month after settlement but only 14.5% of recruits survived to adulthood. Quantifying the magnitude of post-settlement mortality, and accounting for the processes responsible, is thus pivotal for accurately predicting how many arriving propagules will survive the introduction phase and successfully survive to establish an adult population.

Controlled experiments testing the relationship between propagule pressure and community traits are increasing, but are more common in terrestrial ecosystems (Tilman 1997; Forsyth and Duncan 2001; Foster 2001; Colautti et al. 2006; Simberloff 2009). In the marine realm, artificially enhancing propagule supply in the field can be challenging, especially in subtidal environments (Johnston et al. 2009). Nonetheless, manipulations have been conducted for five species: two bryozoans, *Bugula neritina* (Clark and Johnston, 2005) and *Watersipora subtorquata* (Clark and Johnston 2009, 2011), the bivalve *Crassostrea gigas* (Hedge et al. 2012), and two algal species *Sargassum muticum* (Britton-Simmons and Abbott, 2008) and *Undaria pinnatifida* (Valentine and Johnson 2003, 2005). Field experiments with early life history stages of these species have shown that the role of propagule pressure is often co-regulated by other processes including disturbance (Valentine and Johnson 2003; Clark and Johnston 2005, 2009), resource availability (Britton-Simmons and Abbott, 2008) and biotic resistance (Britton-Simmons and Abbott, 2008).

I conducted two experiments to investigate how propagule supply and post-settlement processes affected colonization success of an invasive ascidian. *Botrylloides violaceus*

Oka, 1927 releases free-swimming, lecithotrophic larvae that are relatively large (2-3 mm) and visible to the naked eye (Saito et al. 1981; Mukai et al. 1987), making it an ideal candidate for *in-situ* field manipulations of larval propagules. In the first experiment, I manipulated propagule supply in the field to test how habitat type, community type and propagule number affected establishment success. This manipulation of propagule delivery is the first of its kind using ascidians. I estimated invasion success by measuring the settlement and recruitment (persistence after eight weeks) of *B. violaceus* colonies and compared these between floating and fixed habitats. In the second experiment I pre-seeded plates with newly settled *B. violaceus* colonies and assessed how settler density and access by predators affected post-settlement survival through time. I followed individual colonies for eight months (November 2010-June 2011) from settlement through recruitment and reproductive maturity. These novel approaches to *in-situ* propagule manipulation have not been reported previously (for ascidians) and the combined experiments tested hypotheses on invasion success and the role of propagule number and post-settlement survivorship.

4.3 Methods

4.3.1 Experiment 1: Propagule dosing

Propagule experiments were conducted from August-October 2010 at the Institute of Ocean Sciences (IOS, 48.675,-123.449) on Southern Vancouver Island, British Columbia. I used a three-way factorial design to manipulate habitat type (floating and fixed), community type (established and empty), and propagule number (0, 5, 25 and 50 larvae 225 cm^{-2}) with five replicates per treatment combination. The highest dosing level was equivalent to 2200 individuals per square meter. Dive surveys at IOS in 2008 had previously recorded colonies of *B. violaceus* on the floating docks at a density of 3 colonies m^{-2} (see Chapter 3). The presence of adult colonies meant that there was a background level of larval release at this site but the experiment was designed to take this into account and test whether enhancing larval dose would lead to increased settlement compared to background levels. The floating habitat was the undersides of dock pontoons within a small craft marina, and the fixed habitat consisted of boulders at the base of a breakwater located approximately 15 m away from the marina pontoons. The local bottom substrate was largely composed of mud, sand, and gravel with some eelgrass and a depth range of 1.5 to 4.5 m.

The community type treatment had two levels: an established community or blank tiles. In February 2010, five months prior to starting experimental trials, 20 lightly sanded 15 x 15 x 1 cm PVC tiles were deployed within both the floating and fixed habitats to acquire a fouling community representative of each habitat. Floating tiles were suspended underneath dock pontoons at a depth of 30 cm and fixed tiles were placed at a depth of 2 meters below mean low water among boulders at the base of the breakwater. Tiles were placed horizontally and facing downwards in both habitats to minimize algal growth and enhance invertebrate settlement, mimicking the undersides of floating docks and communities within boulder crevices along the breakwater. Three days prior to beginning experiments, established community plates and blank PVC tiles (used for the empty community treatments) were labelled and randomly assigned to a position within the experimental setup (established floating communities were retained in floating experiments while fixed communities remained in the fixed habitat experiment). This three day period allowed the empty tiles to accumulate a biofilm before larval manipulations began. In the floating habitat, an array of horizontal, downward-facing tiles was attached directly to the underside of floating docks using line and zip-ties (see Figure 4.1a). In the fixed boulder habitat, a similar array of tiles was attached to the underside of large PVC boards (0.5 m width x 1 m length; Figure 4.1b) and deployed horizontally (facing down) among boulders at the base of the breakwater using concrete blocks to keep them level and approximately 30 cm above the bottom substrate. In total, fixed and floating experimental arrays had 40 tiles each and a replicate of each treatment was randomly assigned to a position within each habitat. On the morning of propagule dosing, a circular 16 oz plastic dosing container (10 cm diameter) was attached to the center of each treatment using zip-ties (Figure 4.1c). Approximately 50% of the surface of the dosing containers was removed and replaced with 250 μm plankton mesh to allow water exchange while preventing larval escape.

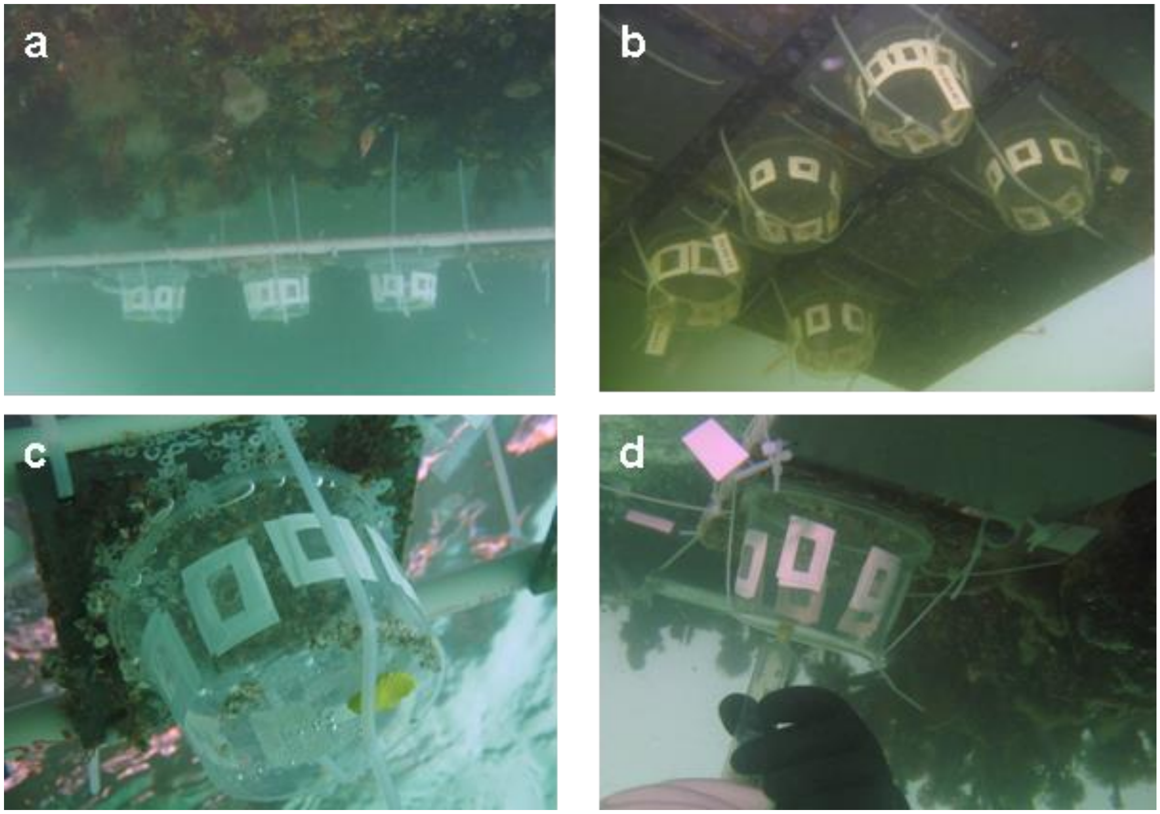

Figure 4.1:Pictures of experimental treatments at the Institute of Ocean Sciences. Figure (a) shows experimental PVC tiles attached below floating docks, the treatments are facing down towards the benthos and have larval dosing containers attached. Figure (b) shows the fixed experimental PVC tiles attached to large PVC backing plates that were then placed 30 cm above nearby breakwater/boulder substrate. Figure (c) shows a close-up of the larval dosing containers with windows of 250 µm plankton mesh and yellow putty covering the opening for larval dosing. Figure (d) shows a diver injecting a syringe of *Botrylloides violaceus* larvae into the experimental treatment.

To acquire propagules for experimental manipulations, adult colonies of *B. violaceus* were collected from pilings and floating docks at the Royal Victoria Yacht Club (48.451,-123.295). Colonies were scraped carefully from fouled surfaces using putty knives, put into sea water containers, placed in a cooler and transported 20 minutes to IOS. Once there they were placed in buckets of seawater where they were agitated, by prodding and altering light conditions, to induce larval release. Once released, larvae were counted and drawn into 60 ml plastic syringes. Only larvae which were actively swimming were used during experiments. Syringes were filled completely with seawater and plugged at the end with putty. They were immediately handed to a SCUBA diver who was waiting in the water. The diver carefully initiated a ‘propagule delivery’ by injecting the contents of the syringe into the appropriate treatment via a small opening in the 16 oz dosing container (Figure 4.1d). To ensure that no larvae remained within the syringe, it was refilled underwater while no larvae could escape the dosing unit and injected an additional two times. The opening was then sealed with plastic putty and containers were left for 24 hours. Larvae of *B. violaceus* swim for minutes to hours before settling (Saito et al. 1981) and waiting 24 hours thereby ensured that all larvae had time to settle. Prior to conducting field experiments, viability tests were conducted in the laboratory to ensure that larvae were not damaged during release from the syringe. In trials, 97% of larvae (n = 300) survived injections and successfully settled and metamorphosed.

After 24 hours the dosing containers were removed and any larvae that settled on the inside of the containers were counted. I assumed that any larvae that did not settle on the inside of the containers, settled on the experimental plates. I verified these values by counting the number of settlers on empty community plates, but it was not possible to reliably count new settlers within established communities *in-situ*. Larval dosing of fixed and floating treatments was carried out under marina docks and arrays fixed to their habitats 24-hours after dosing (post-attachment at the time of container removal). The experimental tiles were left for eight weeks before being retrieved, photographed and all of the *B. violaceus* colonies counted.

4.3.2 Experiment 2: Post-settlement survival

Post-settlement survival experiments of newly settled *B. violaceus* larvae were conducted in November 2010 through July 2011 at Fisherman’s Wharf marina in Victoria, British Columbia (48.423, -123.385). A week prior to the experiments, adult *B. violaceus* colonies were collected from floating docks at the nearby Royal Victoria Yacht Club (48.451,-123.295) using methods described above. Once collected, colonies where transported to the aquatics laboratory at the University of Victoria, where they were kept in flow-through seawater aquaria in a recirculation system at 15°C on a 12hr light/12hr dark cycle. As reported by other authors (Yamaguchi 1975; Epelbaum et al. 2009b), *B. violaceus* tended to spawn shortly after the light-cycle began, beginning around 0800h, and newly released and actively swimming larvae were pipetted onto submerged, lightly sanded, 15 x 15 x 1 cm PVC tiles. Tiles were kept in the dark for 24 hrs to limit light stimulation and ensure that most larvae settled on the tiles, rather than becoming trapped by the surface tension of the water. Once settled, tiles with newly metamorphosed juveniles were placed in flow-through aquaria for up to four days, after which they were photographed and deployed in the field.

A factorial experimental design was used to assess how the density of settlers (5, 10, 20 and >25) and predator access (caged and uncaged) affected post-settlement survival in juvenile *B. violaceus*. Each treatment was replicated four times for a total of 32 experimental tiles. Caged treatments consisted of a PVC tile enclosed within a 1 x 1 cm plastic mesh. The cages were sized to fit snugly around the PVC tiles and were approximately 13 cm in height. Tiles were deployed by hanging eight lines of five tiles each (four treatment tiles and one control tile, all >10cm apart) from the floating pontoons at Fisherman's Wharf. Each line also contained a blank control tile (position along the line was randomized) to assess levels of background larval settlement. Lines were weighted at the bottom with bricks to keep them oriented vertically in the water column. The plates were monitored by taking digital photographs and counting all colonies every three days for the first two weeks (November 1, 2010 – November 16, 2010), then once a week for the following five months (November through April 2011), and once a month during May, June and July 2011. By June, surviving colonies started reproducing and brooding larvae. Digital photographs enabled any newly-settled individuals to be distinguished from those present at the start of the experiment.

4.3.3 Data Analysis

4.3.3.1Propagule dosing

Prior to running parametric tests, data were assessed for normality and homogeneity of variances using Anderson-Darling and Levene tests (α=0.05), respectively. Settlement of *B. violaceus* was measured as the proportion of larvae released which were counted as metamorphosed settlers 24 hours after inoculation (i.e. number of settlers/number of larvae in the syringe). To compare settlement rates across the manipulated experimental factors, settlement data were analyzed using a three-factor ANOVA with the fixed and orthogonal factors habitat type (fixed and floating), community type (established and empty), and propagule dose (0, 5, 25, 50). For floating tiles, to test whether community type (established or empty) or larval dose (0, 5, 25, 50 larvae) had an effect on recruitment success, data were analyzed using a two-way ANOVA. On fixed tiles, very few colonies remained and parametric statistical analysis was not possible. Instead, the non-parametric Scheirer-Ray-Hare test (Dytham, 2003) was used to test whether community type or larval dose had an effect on recruitment in the fixed habitat. For all significant ANOVA results post-hoc differences between groups were tested using Tukey's HSD.

4.3.3.2 Post-settlement survival

Survivorship curves of *B. violaceus* settlers were constructed to show levels of post-settlement mortality throughout the nine month experiment. To test whether initial settler density (5, 10, 25 or > 25 per 15 x 15 cm PVC tile) or access by predators (caged and uncaged tiles) affected survivorship, data were analyzed with a non-parametric Scheirer-Ray-Hare test. Non-parametric Friedman tests were used to investigate differences in the proportion of caged and uncaged colonies surviving through time at each of the settler density levels. These tests utilized the factors time (repeated measures) and predator access (caged and uncaged). All data analyses were performed using MINITAB 15(© Minitab Inc., State College, PA, USA).

4.4 Results

4.4.1 Propagule Dosing Experiments

In-situ larval dosing was successful with an average of 55% (± 2.6 SE) of larvae settling on experimental tiles in the floating and fixed treatments. Twenty-four hours after inoculations, settlement across the experimental trials showed significant differences among larval dosing treatments (three-way ANOVA, $F_{1,59}$= 217.67, $p < 0.001$) with numbers of settlers reflecting the dose-sizes delivered (Figure 4.2). There were no differences between the number of larvae settling on established and empty tiles 24 hours after dosing (three-way ANOVA, $F_{1,59}$ = 0.90, p = 0.349; Table 4.1, Figure 4.2), however larval settlement was significantly lower on fixed plates compared to floating ones (three-way ANOVA, $F_{1,59}$ = 13.32, p>0.001; Table 4.1, Figure 4.2).

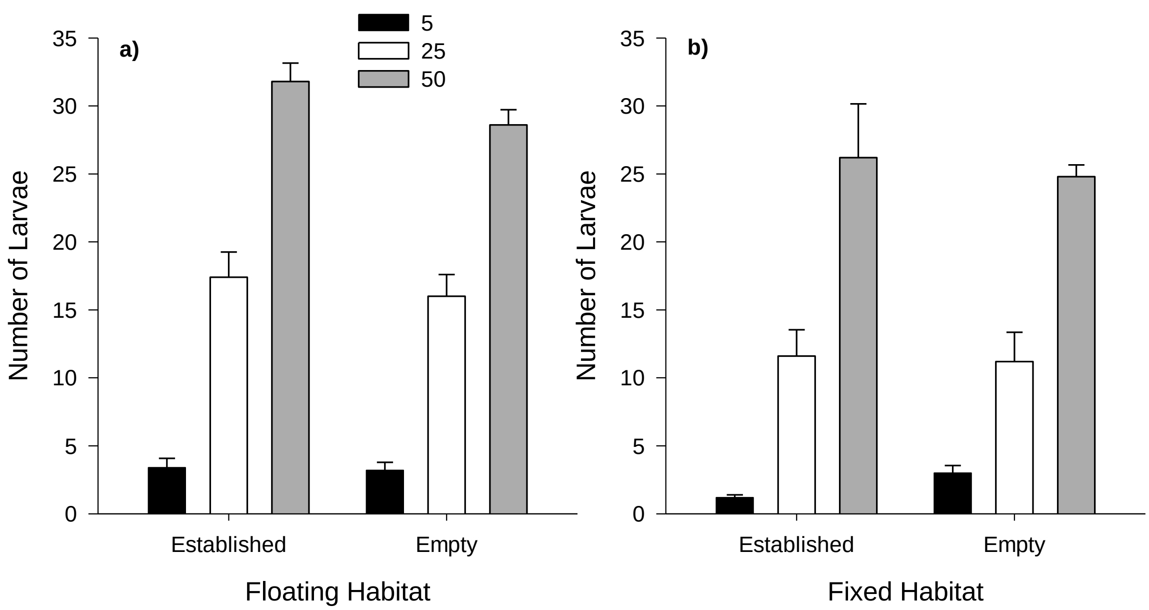

Figure 4.2: The number of larvae settled on established and empty community experimental plates 24-hours after larval dosing.

Table 4.1: A three-way Analysis of Variance comparing settlement in *Botrylloides violaceus* 24 hours after larval release. Habitat is fixed and orthogonal with two levels: floating and fixed. Community type is fixed and orthogonal with two levels: established and empty. Larval dose is fixed and orthogonal with three levels: 5, 25 and 50 larvae.

Source of variation	df	MS	*F*	p
Habitat	1	194.40	13.32	**<0.001**
Community	1	13.07	0.90	0.349
Larval Dose	2	3176.15	217.67	**<0.001**
Habitat * Community	1	13.07	0.90	0.349
Habitat * Larval Dose	2	21.65	1.48	0.237
Community * Larval Dose	2	12.52	0.86	0.43
Habittat * Community * Larval Dose	2	0.02	0	0.999
Error	48	14.59		
Total	59			

Fifty-six days after larval inoculations there was a striking difference in the number of recruits between habitats, with very few *B. violaceus* colonies remaining on fixed treatments which were close to the benthos (Figure 4.3). In floating habitats, it was clear that background inputs of *B. violaceus* larvae were being delivered to experimental units, most likely from adult colonies on nearby structures. Although the number of background larvae that settled to each treatment was not continuously measured throughout the experiment, monitoring one-week after larval dosing revealed that the five floating control tiles had 3, 2, 4, 0, and 0 larvae present ($\bar{x}$ = 2) respectively, and the five fixed control tiles had no larvae present. On floating tiles, dose size had no effect on recruitment success(two-way ANOVA, $F_{1,39}$ = 1.80, p = 0.167; Table 4.2, Figure 4.3), suggesting that background levels of settlement were large and variable enough to mask any possible effect of larval dosing, even though tiles dosed with 50 larvae had the highest average number of settlers (Figure 4.2). In fixed habitats, community type (Scheirer-Ray-Hare, H = 0.001, p = 0.977) and larval dose (Scheirer-Ray-Hare, H = 6.7011, p = 0.082; Table 4.3, Figure 4.3) had no significant effect on recruitment success. Recruitment on fixed tiles after 56 days was zero across all control and 5-larvae-dose treatments. *B. violaceus* colonies were recorded on fixed-habitat replicates of 25-larvae and 50-larvae doses, although only the latter had larvae on both established and empty replicates.

Table 4.2:A two-way Analysis of Variance comparing recruitment of *Botrylloides violaceus* on floating treatments 56 days after larval dosing. Community type is fixed and orthogonal with two levels: established and empty. Larval dose is fixed and orthogonal with four levels: 0, 5, 25 and 50 larvae.

Source of variation	df	MS	*F*	p
Community	1	2.02	0.08	0.778
Larval Dose	3	44.89	1.80	0.167
Community * Larval Dose	3	11.76	0.47	0.705
Error	32	24.96		
Total	39			

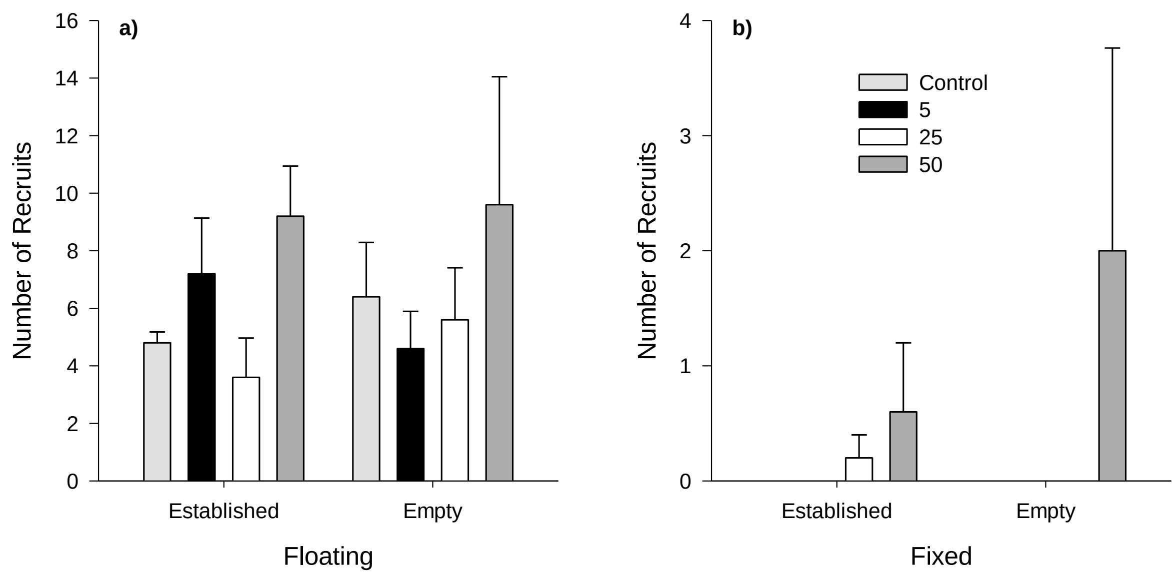

Figure 4.3:The number of recruits present on experimental treatments of different community types (established and empty) within two habitats (floating and fixed) 56 days post-inoculation.

Table 4.3: Scheirer-Ray-Hare test comparing recruitment success in *Botrylloides violaceus* on fixed treatments 56 days after larval dosing. Community type has two levels: established and empty and Larval dose has four levels: 0, 5, 25 and 50 larvae.

Source of variation	df	SS	MS	*H*	p
Community	1	2.02		0.08	0.778
Larval Dose	3	44.89		1.80	0.167
Community * Larval Dose	3	11.76		0.47	0.705
Total	39		37.04		

4.4.2 Post-settlement Survival

A total of 551 newly settled *B. violaceus* were placed in the field to assess survival over time. After four days, 52% (n = 285) remained. Within two weeks of deployment, on day 15, only 9% (n = 51) of the settlers were still present. At the end of the experiment, after 252 days in the field, only 1% (n = 5) survived to be reproductive. The starting density of settlers (5, 10, 20 or > 25 per 15 x 15 cm PVC tile) did not affect long term survivorship (Scheirer-Ray-Hare, H = 2.214, p = 0.529), but access by predators did (Scheirer-Ray-Hare, H = 4.429, $p < 0.05$; Figure 4.4). All five colonies remaining at the termination of the experiment were on caged predator-exclusion tiles. Survivorship of colonies through time at the five settlers per tile treatment did not differ between caged and uncaged treatments (Friedman Test, S = 0.31, p = 0.715), whereas settlers at the 10, 25 and >25 settler treatments had greater survivorship on caged tiles than uncaged tiles (Friedman Test, S = 28.03, $p < 0.001$; Figure 4.5).

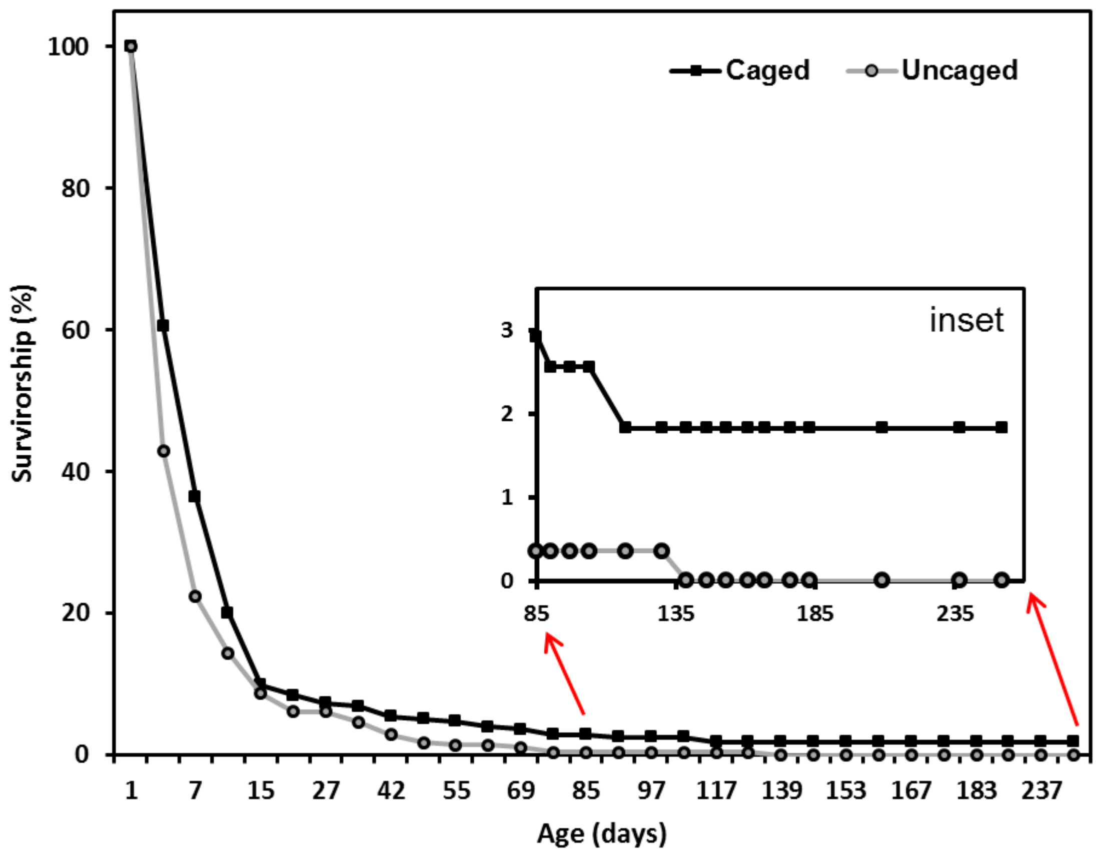

Figure 4.4: Survivorship of *Botrylloides violaceus* in caged (n =274) and uncaged treatments (n =277).

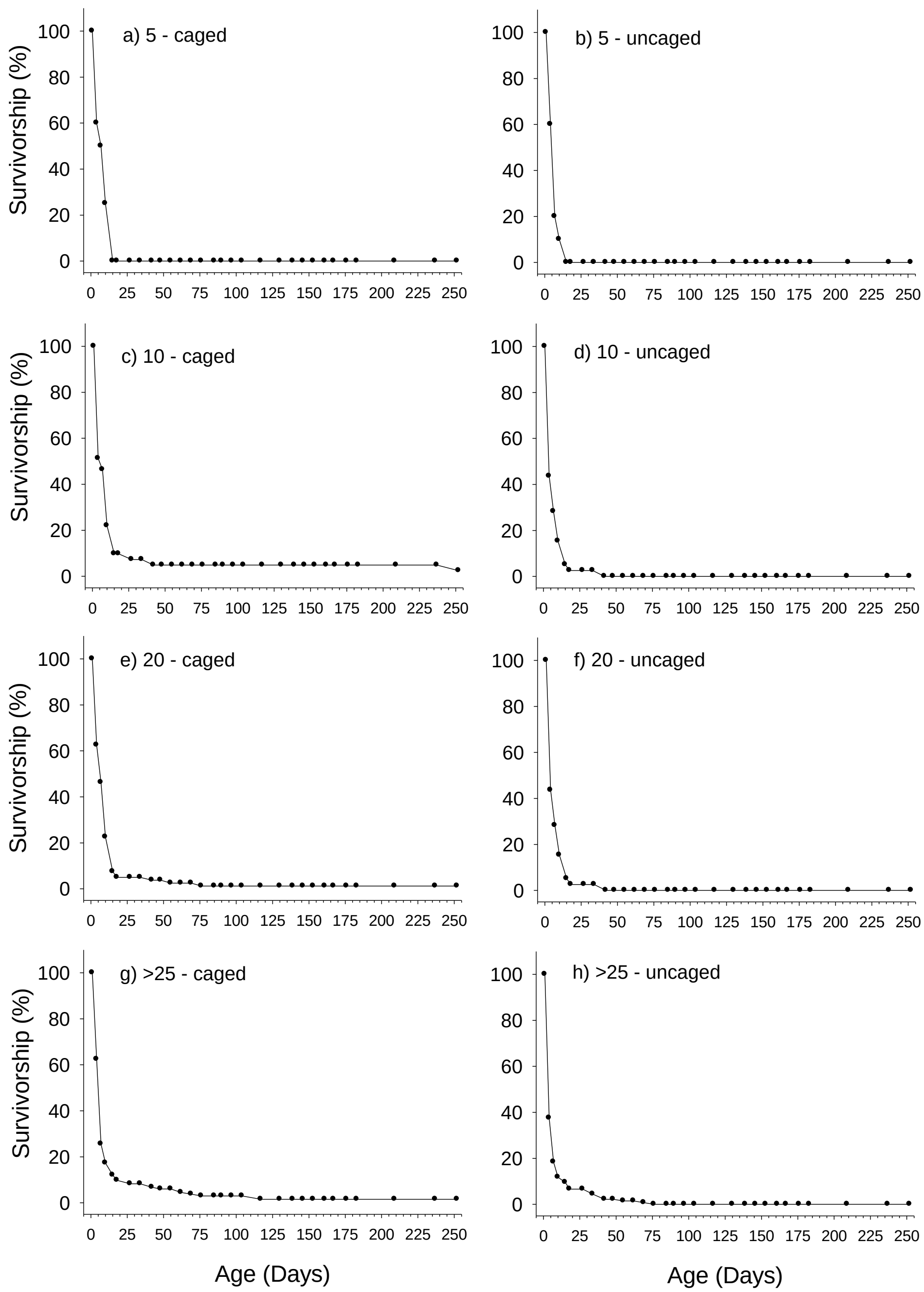

Figure 4.5: Survivorship of *Botrylloides violaceus* at each density (5, 10, 20 and > 25 settlers) and predator (caged, uncaged) treatment.

4.5 Discussion

4.5.1 Propagule Dosing Experiment

Propagule pressure encompasses two components: the number of individuals released per introduction event (termed propagule number), and the number of introduction events (termed propagule frequency) (Cassey et al. 2004). The propagule pressure experiment directly manipulated one of these components – propagule number. There was a clear (and expected) effect of larval dose-size on initial settlement of *B. violaceus*, which subsequently disappeared for the range of dose-sizes used in this experiment. Although the uppermost dose-size was the equivalent of 2200 larvae m^{-2}, an effect of propagule number was not recorded after 56 days because (a) the maximum dose-size and differences between doses may not have been large enough to have an effect; (b) the differences between treatments that emerged initially may have been masked by the background frequency of larval release over time (e.g. in floating habitats); or (c) survivorship may have been low regardless of dose-size and initial settlement (in fixed habitats).

It is not clear how large a difference between inoculation sizes is required for detecting *B. violaceus* colonization differences over time. Previous studies of this type of experiment used a range from 30 to 90 larvae for bryozoans (Clark and Johnston, 2005; 2009; 2011), 500 to 8000 oyster larvae (Hedge et al. 2012), and up to an estimated 5 million propagules for algae (Valentine and Johnson 2003, 2005; Britton-Simmons and Abbott, 2008). The range of dose sizes approximated those of the bryozoans and was also determined by the accessibility to larvae for all treatments and replicates. The issue of background larval release was confirmed by the presence of *B. violaceus* colonies on control tiles in floating habitat at the end of the experiment. Despite the precautions to remove *B. violaceus* colonies in the vicinity of tiles, it appears that the remaining colonies resulted in additional larval numbers and variations in propagule frequency over the eight weeks of the experiment. Recent research using oyster larvae showed that increasing the frequency of larval introduction can result in greater recruitment and persistence (Hedge et al. 2012). While the maximum dose had the highest average recruitment, with up to 9 colonies persisting per tile, the effect of unmeasured variation in larvae frequency meant that these were not significantly different from the zero-dose treatments. Further experiments varying both the number and frequency of *B. violaceus* larvae are needed to determine the relationship between propagule pressure and establishment in this species.

Although background larval release may have swamped any effect of dose-size for floating tiles (near the marina pontoons), this was not recorded in fixed benthic habitat. No larvae appeared to be able to disperse from floating habitats (which had established adult colonies present) to fixed habitats, because I did not record any on the control plates (and did not see any recruitment to adjacent rocks). In order for a species to spread beyond its initial introduction location it needs to overcome barriers to dispersal (Carlton 1996b). In this system, propagule pressure to nearby natural habitats may be low. Larvae of *B. violaceus* are present in the water column for only minutes to hours (Saito et al. 1981) thus limiting their ability to disperse over great distances (Shanks, 2009). In addition, larvae of many ascidian species are gregarious and the presence of conspecific individuals can encourage settlement near other established juveniles or adults (Peterson and Svane, 1995; Rius et al. 2010). However, research on colonial didemnid ascidians, which have larval durations of 2-36 hours, show that at some current speeds larvae may disperse up to 250 m (Olson, 1985; Fletcher et al. 2013). Nevertheless, the experiment was conducted in a marina partially enclosed by a breakwater, which may limit the amount of water movement around structures (Floerl and Inglis, 2003). I did not record any larval or adult occurrence in fixed habitats at IOS over two years (Simkanin C. unpublished data). As populations of *B. violaceus* continue to successfully establish and propagate on floating structures, the chance that propagules will escape marina environments and traverse the short distance to nearby benthic rocky habitat increases. In the face of anthropogenic changes, such as increased water temperatures, *B. violaceus* has been shown to increase its growth and reproduction (Epelbaum et al. 2009a, Dijkstra et al. 2011), potentially increasing population sizes, propagule release and the likelihood of successful establishment beyond marina boundaries.

At the end of the eight-week propagule pressure experiment the difference in survival between *B. violaceus* recruitment on floating and fixed habitats was large (Figure 4.3). Very few settlers survived on fixed tiles, and the few that did remain were from the higher larval dose treatments (i.e. 25 or 50 larvae). Because the fixed tiles were close to the benthos they may have been more easily accessible to local benthic predators (e.g. sea stars and crustaceans) than floating habitat tiles (Dumont et al. 2011a; Cordell et al.in press). This was observed at the completion of the experiment, when a number of sea stars were found attached to the fixed tiles. Interspecific post-settlement interactions such as predation and competition have been shown to greatly increase mortality rates in marine ecosystems (Gosselin and Qian, 1997; Mitcheli et al.2002; Osman and Whitlatch, 2004); and in a review of the literature, Hunt and Scheibling (1997) found that predation was the most documented cause of post-settlement mortality in benthic marine invertebrates. Predation may be a significant factor limiting the spread of this species to nearby natural rocky habitats (Chapter 3).

Some studies have shown that resource availability is a principal causal agent governing invasibility (Davis et al. 2000; Clark and Johnson 2005; Davis 2009; Clark and Johnson 2011); however this result did not bear out during this study. Empty community panels with high amounts of free space did not differ from established community panels in the number of *B. violaceus* recruits at the end of eight weeks (Figure 4.3). Although space is a major limiting resource in epifaunal communities (Dayton 1971, Sutherland 1978), colonial ascidians have the ability to settle and grow on secondary substrate such as algae, bivalve shells, and other ascidians (Saito et al. 1981; Svane and Young 1989; Berman et al. 1992; Dijkstra et al. 2007). This ability may be a factor contributing to their invasion success in varying environments around the world (Chapter 3), and certainly contributes to their ability to settle and overgrow aquaculture species (McKindsey et al. 2007).

4.5.2 Post-settlement Survival

After four days in the field, nearly half of the 551 newly settled *B. violaceus* colonies had perished. This sharp decline in survival likely resulted from rapid physical and behavioral changes as colonies adjusted to their new environment (Gosselin and Qian, 1996; 1997). Although mortality continued through time, access by predators appeared to be the predominant factor affecting survivorship. Density- dependent survivorship has been shown for some newly settled sessile species (Hunt and Scheibling, 1997), including ascidians (Marshall and Keough, 2003); however there was no effect of density on survivorship in this experiment. Overall, post-settlement survival in *B. violaceus* was low, with only 1% of the introduced colonies (5 of 551) surviving to reproductive maturity. This high level of mortality is not unusual when compared with other benthic marine invertebrate species. In a review by Gosselin and Qian (1997), 17 of the 30 papers examined had juvenile mortality ≥ 98%. This included research on bivalves, gastropods, ascidians, bryozoans and echinoderms.

Rates of post-settlement mortality may vary depending on the timing of larval release. For instance, beyond intra- and inter-specific interactions, physical factors such as environmental disturbances can also influence the success of early life stage recruits (Gosselin and Qian, 1997). In this study, experimental trials began in November and only 1% of the initial settlers survived through the winter (November 2010-March 2011). This 1% (or five colonies) continued to survive until the termination of the experiment in June. The larvae utilized for this experiment were some of the last of the reproductive season, which typically ranges from early June to late October for this species in British Columbia (Epelbaum et al. 2009b). By being released in November, newly settled individuals immediately experienced cooling temperatures that likely fall outside the tolerance limits of such young juveniles (Epelbaum et al. 2009a). It is more likely that settlers released at the beginning of the reproductive season in June, when environmental conditions are more amenable to growth and survival (Epelbaum et al. 2009a) will persist. Therefore, in order to determine the likelihood of successful establishment of a species, post-settlement survivorship should be investigated at varying times of year. This may help determine how phenology helps to predict the windows of opportunity that exist for successful invasion events.

4.5.3 Experimental methods

The methods utilized in this experiment demonstrated that it is possible to successfully introduce viable ascidian larvae into field experiments. Only a few previous studies have successfully enhanced invertebrate propagule supply in the marine environment (Clark and Johnston 2005, 2009, 2011; Hedge et al. 2012), and none have used ascidians as target species. Using ascidians in these types of dose-size manipulations can be insightful for both basic and applied research into early-stage invasion dynamics and management, as long as access to sufficient quantities of larvae is possible. This methodology may be expanded to utilize other ascidian species and to test various hypotheses regarding intra- and inter- specific supply-side ecology.

However, logistical hurdles remain. It is usually not permissible to conduct an experiment of this nature at a site that has not been invaded, in case the experiment facilitates an invasion. Therefore the effect of already present colonies or adults would have to be monitored closely during the experiment or even more rigorous suppression of the established colonies would be required. Even if this issue was overcome, the practicality of collecting sufficient numbers of larvae, which are only viable in the water column for a few hours, can be a challenge. The target species in this study, *B. violaceus*, is a colonial species which broods live young, so procuring propagules is reliant on inducing colonies to release larvae. However, if solitary ascidians are used, strip-spawning (see Marshall et al. 2000 and Rius et al. 2009 for technique) can allow a researcher to artificially fertilize gametes, supplying many larvae relatively quickly and potentially allowing for experiments with higher dosing levels than those used here (i.e. > 50 larvae 2200 larvae m^{-2}).

4.5.4 Conclusions

Determining which factors affect establishment success in newly arriving species is a key goal for ecologists and invasion biologists alike (Simberloff and Wilson, 1969; Sakai et al. 2001). Propagule pressure is considered one of the most important factors determining establishment success of an invader (Simberloff 2009). The present study demonstrated that post-settlement mortality in *B. violaceus* is high and that large numbers of larvae or frequent introduction events may be needed for successful invasion. A combination of factors, including habitat type, predation and possibly the seasonal timing of propagule release, can affect establishment in this species. Further study is needed to determine the relative importance of these factors in the establishment process. The in-situ inoculation method used is ideal for testing invasion models in subtidal environments (Clark and Johnson 2005; 2009) and can be utilized to explore the link between propagule pressure (including number and frequency) and invasion success for a number of sessile marine invertebrates including ascidians. Testing this relationship provides critical insight into the factors that affect establishment, which is essential for predicting and managing invasions.

Chapter 5: Biotic resistance to the infiltration of natural benthic habitats: examining the role of predation in the distribution of the invasive ascidian *Botrylloides violaceus**

5.1 Abstract

Anthropogenic marine habitats, such as marinas and breakwaters, are frequently colonized by nonindigenous species (NIS). Comparative studies show that few sessile NIS are found in nearby natural habitats, but little is known about the processes affecting spread into these habitats. In southern British Columbia, the invasive colonial ascidian *Botrylloides violaceus* is widespread, but is far more common on man-made structures at marinas and aquaculture facilities than adjacent natural rocky reefs. To determine whether predation by native species, one element of biotic resistance, influences the successful infiltration of *B. violaceus* into natural benthic habitats, I conducted a series of predator exclusion experiments. Established adult colonies and newly settled juvenile *B. violaceus* were transplanted onto replicate PVC panels and deployed at marina pilings and adjacent natural rocky reefs at two locations. Panels were assigned to caged, uncaged, and procedural control treatments to test whether predator exclusion changed survivorship. Both juvenile and adult ascidian survival was significantly lower in uncaged treatments, suggesting that predation can limit the abundance and distribution of this species. Results were similar between piling and rocky reef habitats regardless of life stage and results suggest that adult and juvenile *B. violaceus* are vulnerable to predation in both habitats studied. If *B. violaceus* propagules can disperse from dock floats and infiltrate adjacent natural rock, biotic resistance, through predation by native species, may diminish the likelihood of successful colonization in these habitats. Ensuring that natural habitats and native benthic communities remain healthy and intact may reduce the likelihood that invasive ascidians will spread beyond anthropogenic introduction sites where they can dominate the fouling community.

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5.2Introduction

The introduction and spread of nonindigenous species (NIS) has altered the composition of marine assemblages around the globe (Carlton, 1989; Galil, 2007; Costello et al. 2010).In particular, anthropogenic habitats, such as marinas, wharfs and aquaculture facilities, appear to be focal points for invasions (Ruiz et al. 2009; Bulleri and Chapman, 2010). These structures are directly associated with human-mediated vectors that transport nonindigenous propagules and are often the first site of contact for NIS transferred by commercial ships, recreational boats, and aquaculture shipments. The link between artificial structures and NIS establishment is particularly important for sessile species which need hard stable surfaces for settlement (Lambert, 2007; Ruiz et al. 2009). In such environments, sessile NIS can reach high densities, covering most of the available structure, and often outnumbering native species (e.g. Lambert and Lambert, 2003). Studies comparing the distribution of sessile NIS in anthropogenic and nearby natural habitats have shown that some species have spread, but most have not infiltrated natural benthic ecosystems (see Lambert, 2002; Glasby et al. 2007; Simkanin et al. 2012). This pattern appears consistent across studies, but little is known about the underlying ecological processes that influence the connection between anthropogenic and nearby natural habitats.

The ability of a NIS to establish in different habitats is dependent on a range of biotic and abiotic factors (Lonsdale, 1999; Levine et al. 2004), including the prevalence of native generalist predators in the receiving environment (Lawton and Brown 1986; Gruner 2005). Predation by native species on nonindigenous prey, one element of biotic resistance, can regulate the establishment, spread, and habitat use of an invader (Reusch, 1998; Byers, 2002; Ruesink, 2007; Dumont et al. 2011a).Predator-prey interactions may exclude an invader from successfully establishing in a new region (Schoener and Spiller, 1995), but may also limit a species ability to propagate and spread from an initial introduction site (i.e. moving from the establishment to the spread stage, as in Blackburn et al. 2011). For example, in a large scale study, deRivera et al. (2005) found that predation by the native crab, *Callinectes sapidus* Rathbun, 1896 could limit the southward spread of the nonindigenous crab, *Carcinus maenas* (Linnaeus, 1758) on the U.S. East Coast.

Although predation can influence the long term dynamics of an invasion (Colautti et al. 2004; Carlsson et al. 2009), little is known about whether native predators may limit the localized spread(10^0 – 10^2 m) of sessile NIS from anthropogenic to natural habitats. The abundance of benthic predators can differ substantially between anthropogenic and nearby natural habitats (Dumont et al. 2011b). Artificial structures, especially those that lack structural complexity or which are separated from natural substrates, may have a lower abundance of mobile predators (Chapman, 2003; Chapman and Blockley, 2009; Dumont et al. 2011a, b) and therefore may act as refuges for the establishment of NIS. In natural habitats, where generalist predator numbers are greater, there may be increased invasion resistance to newly arriving propagules.

Nonindigenous ascidians often dominate the sessile invertebrate fauna on artificial structures (Lambert and Lambert, 1998; Lambert and Lambert, 2003). Some of these species are highly invasive with increased global concern about their potential economic and ecological impacts (Lambert, 2007; McKindsey et al. 2007).*Botrylloides violaceus* Oka, 1927, a colonial ascidian native to the Northwest Pacific (Lambert and Sanamyan, 2001), is a highly successful invader having established populations in temperate regions around the globe. In its introduced range on the East coast of the U.S., *B. violaceus* has been documented in anthropogenic and natural habitats, where it can be a strong competitor for space. It grows rapidly, overgrowing primary and secondary habitat, and quickly becomes competitively dominant over other invertebrate species (Berman et al. 1992; Dijkstra et al. 2007; Miller and Etter 2011). Field studies conducted in this region have shown that native predators, such as sea urchins (Simoncini and Miller, 2007) and small predatory gastropods (Whitlatch and Osman, 2009) rarely prey on *B. violaceus*.

In British Columbia (B.C.), where *B. violaceus* was first reported in 1992 (Cohen, 2005), it is currently the most widely distributed nonindigenous ascidian on anthropogenic structures, occurring in higher densities than other native and nonindigenous ascidian species (Gartner, 2010). In some areas it has successfully infiltrated natural habitats, but its distribution in natural rocky reefs is limited (Simkanin et al. 2012, Chapter 3). It is far more dominant on, and in most bays restricted to, marina floats, pilings, and aquaculture installations. The high abundance of this species in anthropogenic environments and limited abundance on natural substrates suggest that some factor (or suite of factors) may be limiting its infiltration of adjacent natural rocky reefs. My objective was to test the effect of predation on *B. violaceus* colonies in anthropogenic habitats where it is abundant and subtidal rocky reefs where it is rare. Specifically, I conducted a series of predator exclusion experiments to test: (i) whether mobile benthic predators prey on *B. violaceus* on dock pilings and subtidal rocky reefs; (ii) whether predation rates vary between anthropogenic and natural habitats; and (iii) whether one life-stage (newly settled juveniles or adults) is more susceptible to predation than another. I examined these results and assessed how predation affects the current distribution of *B. violaceus* in B.C., and whether biotic resistance, through predation, limits the spread of this species to natural benthic habitats.

5.3 Methods

5.3.1 Study sites

During the months of July and August in 2009 and 2010, experiments were conducted in two habitat types (marina pilings and adjacent rocky reefs) at two locations on Southern Vancouver Island, B.C., Canada. The two locations were the Royal Victoria Yacht Club (RVYC) in Cadboro Bay, Victoria (48.451º,-123.295º), and the Institute of Ocean Sciences (IOS) in Patricia Bay, Sidney (48.675º,-123.449º). Both locations included a marina enclosed by a man-made breakwater and surrounded by adjacent natural shallow subtidal rocky reef. Rocky reefs were located within 200 m of the marinas. At both locations, marina pilings were made of creosote treated wood and situated on sand and muddy substrate. Rocky reefs were composed of outcrops of bedrock, with intermittent areas of boulder rocky scree and sand. SCUBA surveys, conducted at both locations in 2008, showed that *B. violaceus* was present at RVYC and IOS marinas, but absent from adjacent rocky reefs (Simkanin et al. 2012, Chapter 3). Specifically, at RVYC *B. violaceus* was recorded at a mean density of 7 colonies m-2 on the undersides of dock floats and 2 colonies m-2 on the subtidal portions of pilings, while at IOS *B. violaceus* was recorded at a mean density of 3 colonies m-2 on dock floats and was absent from pilings.

5.3.2 Collection of adult and juvenile *Botrylloides violaceus*

Adult colonies of *B. violaceus* were collected from pilings and floating docks at both marina sites using SCUBA. Colonies were scraped carefully off fouled substrates using putty knives. Once at the surface, some colonies where stored in coolers for transport back to the lab, while other colonies were immediately attached to the center of 15 x 15 cm PVC tiles using hair-nets and rubber-bands. To allow colonies to regenerate and attach, PVC tiles were hung vertically from a line at the marina docks. After one week, about 50% of the ascidians had survived and successfully reattached themselves to the PVC tiles. At this point, hair nets and rubber bands were removed and dead or dying ascidians were discarded so that only viable and growing colonies were used in experimental treatments.

Juvenile colonies were obtained in the laboratory. Adult colonies from both sites were brought back to the aquatics facility at the University of Victoria, where they were kept in flow-through saltwater aquaria in a recirculation system at 15°C on a 12 hr light/12 hr dark cycle. The ascidians tended to spawn shortly after daylight beginning around 8 AM. Forty newly released and actively swimming larvae were pipetted onto submerged 15 x 15 cm PVC tiles and kept in the dark for 24 hrs. Keeping the ascidian larvae covered and without light stimulation ensured that most larvae settled on the tiles, rather than the surface tension of the water. Once settled, juvenile tiles were placed in flow-through aquaria for up to four days, after which individuals were randomly removed for a constant number of 20 juveniles per tile. All juvenile plates were deployed in the field within seven days of settlement.

5.3.3 Predator exclusion experiments

At each of the four experimental sites (two anthropogenic and two natural), adult and juvenile PVC tiles were randomly assigned to one of three treatments (full cage, partial cage, no cage) with four replicates of each. In 2009, full cage treatments consisted of 1 cm x 1 cm plastic mesh. Cages kept the larger stages of sea stars, crabs and fish from plates, but not smaller organisms, and a number of predatory animals were found within treatments. To reduce the likelihood that smaller predators (< 1 cm) were increasing mortality within cages, we ran a second experiment in 2010 using 0.15 cm x 0.15 cm screening mesh. The 0.15 cm x 0.15 cm mesh size excluded all predator groups noted above in addition to predators between 1 cm and 0.15 cm in size, such as nudibranchs, chitons, and flatworms. In each year, partial cage treatments consisted of a cage with half of the roof, half of one side, and one whole side removed. Partial cages acted as a procedural control and were designed to control for hydrodynamic changes created by the cage while still allowing access by predators.

To account for variability in predator abundance throughout the two different habitats I utilized a randomized block experimental design. In the two marinas, PVC plates were attached to dock pilings, 1 m from the sea floor with one of each treatment (full cage, partial cage, and no cage) attached to a single piling. Adult and juvenile plates were deployed separately on randomly chosen pilings within a 20 m^2 area of the marina. Individual pilings were considered blocks for the experimental design and were spaced approximately 3 – 4 m apart. In natural rocky reefs, each PVC plate was attached to an individual 15 cm x 15 cm x 6 cm concrete paving stone using cable ties. The stones were placed upright with the PVC tiles facing outwards and positioned flush with reef rock or boulders 2 – 3 m below Mean Low Water. Groups of plates were considered blocks for the experimental design and were arranged approximately 3 m apart with one of each treatment (full cage, partial cage, and no cage) grouped together. Adult and juvenile plates were grouped separately but distributed randomly along the reef at the appropriate depth. Experiments were run for three weeks and monitored weekly. Observations of potential predators around or inside cages were recorded during each sampling event. To estimate the number and diversity of potential predators, the presence of crabs, shrimp, sea stars, nudibranchs, flatworms, and fish was recorded at each site. Observations were made by divers underwater and individuals were identified to species if possible.

5.3.4 Data analysis

Digital photographs were taken of adult and juvenile plates before and after the three week field deployment. For juvenile ascidians, all plates began with 20 newly settled colonies (< one week old at deployment). Remaining juvenile ascidian colonies were counted at the end of the experimental period and analyzed as the number of colonies surviving per plate. For adult ascidians, percent cover was measured for each plate at the beginning and end of the sampling period using ImageJ 1.41 (U.S. National Institutes of Health, Bethesda, MD, USA). The difference in percent cover during the two time periods was measured as percent survival per plate. Some ascidian colonies (most notably in full cage treatments) grew during the three week experiment, but for analysis, survival was recorded to a maximum of 100 percent.

Statistical analyses were carried out using MINITAB 15(Minitab Inc., State College, PA, USA). Data were assessed for normality and homogeneity of variances using Anderson-Darling and Levene tests (α=0.05), respectively. If data did not meet assumptions of parametric tests they were $\log_{10}$ or angular transformed. In some cases, raw data were negatively skewed and were reflected prior to transformation to meet parametric assumptions (Quinn and Keough, 2002). Test for differences between years were not done because they were different experiments using different mesh sizes. Survival for adult and juvenile *B. violaceus* at IOS in 2009 was extremely low (i.e., often 0) so data are presented (see Figures 5.1 and 5.2) but could not be tested statistically. To test the effect of habitat type and cage treatment on survival of *B. violaceus* I conducted two-way fixed effect ANOVA's with a blocking factor for each location per year (e.g. RVYC in

2009). Tests for effects on juveniles and adults were run separately. To test whether predation rates were greater on juvenile or adult ascidians I carried out two-way fixed effect ANOVA's with habitat and life stage as factors. The response variable was percent survival of juvenile and adult ascidians in uncaged experimental treatments. For all ANOVA tests, when results were significant, post-hoc pairwise comparisons using Tukey's HSD were conducted to determine differences between groups. To account for multiple testing of the data and the subsequent potential increase in Type I error, the alpha of the tests was raised to the significance level $\alpha = 0.01$. Chi-square (χ^2) goodness of fit tests were used to test for significant differences between the abundance of predators between sites.

5.4 Results

5.4.1 Predator Exclusion Experiments

Survival of juvenile and adult *B. violaceus* was significantly greater in fully caged treatments than in uncaged treatments, indicating that predation decreases survival and may be an important factor determining the distribution of this species (Table 5.1, Figures 5.1 and 5.2). There were no differences in survival between pilings and rocky reefs and no interactions between habitat type and treatment. These results were consistent between locations (RVYC and IOS) during both years (2009 and 2010). Survival of ascidians in uncaged treatments was rarely zero (Figures 5.1 and 5.2); however, suggesting that predation does not completely limit survival, at least after three weeks. In every experimental trial except one (RVYC-2009, adults), partial cage treatments were significantly different from full cage treatments ($P < 0.01$) and not significantly different from uncaged treatments ($P < 0.01$; Figures 5.1 and 5.2). In most of the experiments (except for RVYC-2009, juveniles), full cage treatments also exhibited some mortality (Figures 5.1 and 5.2) suggesting that caging may have had some effect on water flow and/or sedimentation levels that affected ascidian survival.

Adult survival in uncaged treatments was higher than that of juveniles in 2009 at RVYC (two-way ANOVA, $F_{1,15} = 12.71$, $p < 0.004$; Figure 5.3, Table 5.2), suggesting a possible preference for juvenile life stages by benthic predators at this location. However, this pattern was not evident at the RVYC in 2010 or at IOS in 2010. In experiments run at both locations in 2010, survival did not differ between life stages (Figure 5.3).

Table 5.1:Two-way (habitat, treatment) ANOVAs with blocking factor for *Botrylloides violaceus* survival in predator exclusion experiments. Bold values indicate statistical significance (P <0.01).

	Juvenile *B. violaceus*				Adult *B. violaceus*			
	df	SS	F	*P*	df	SS	F	*P*
2009 RVYC								
Habitat	1	0.27	5.69	0.030	1	2562.20	5.95	0.028
Treatment	2	2.76	29.25	**0.001**	2	17462.30	20.26	**0.001**
Block (habitat)	3	0.01	0.10	0.960	3	496.00	0.38	0.766
Habitat * Treatment	2	0.25	2.61	0.107	2	280.70	0.33	0.727
Transformation	reflected, $\log_{10}$				none			
2009 IOS	Test not possible				Test not possible			
2010 RVYC								
Habitat	1	28.17	3.42	0.084	1	60.30	0.23	0.640
Treatment	2	403.08	24.45	**0.001**	2	5417.70	10.22	**0.002**
Block (habitat)	3	4.83	0.20	0.898	3	458.60	0.58	0.639
Habitat * Treatment	2	4.08	0.25	0.784	2	82.60	0.16	0.857
Transformation	none				Arcsine Sqrt			
2010 IOS								
Habitat	1	0.14	4.59	0.049	1	300.60	0.73	0.405
Treatment	2	0.54	7.43	**0.005**	2	8933.70	10.92	**0.001**
Block (habitat)	3	0.20	2.11	0.142	3	188.80	0.15	0.926
Habitat * Treatment	2	0.01	0.19	0.826	2	67.10	0.08	0.922
Transformation	reflected, $\log_{10}$				Arcsine Sqrt			

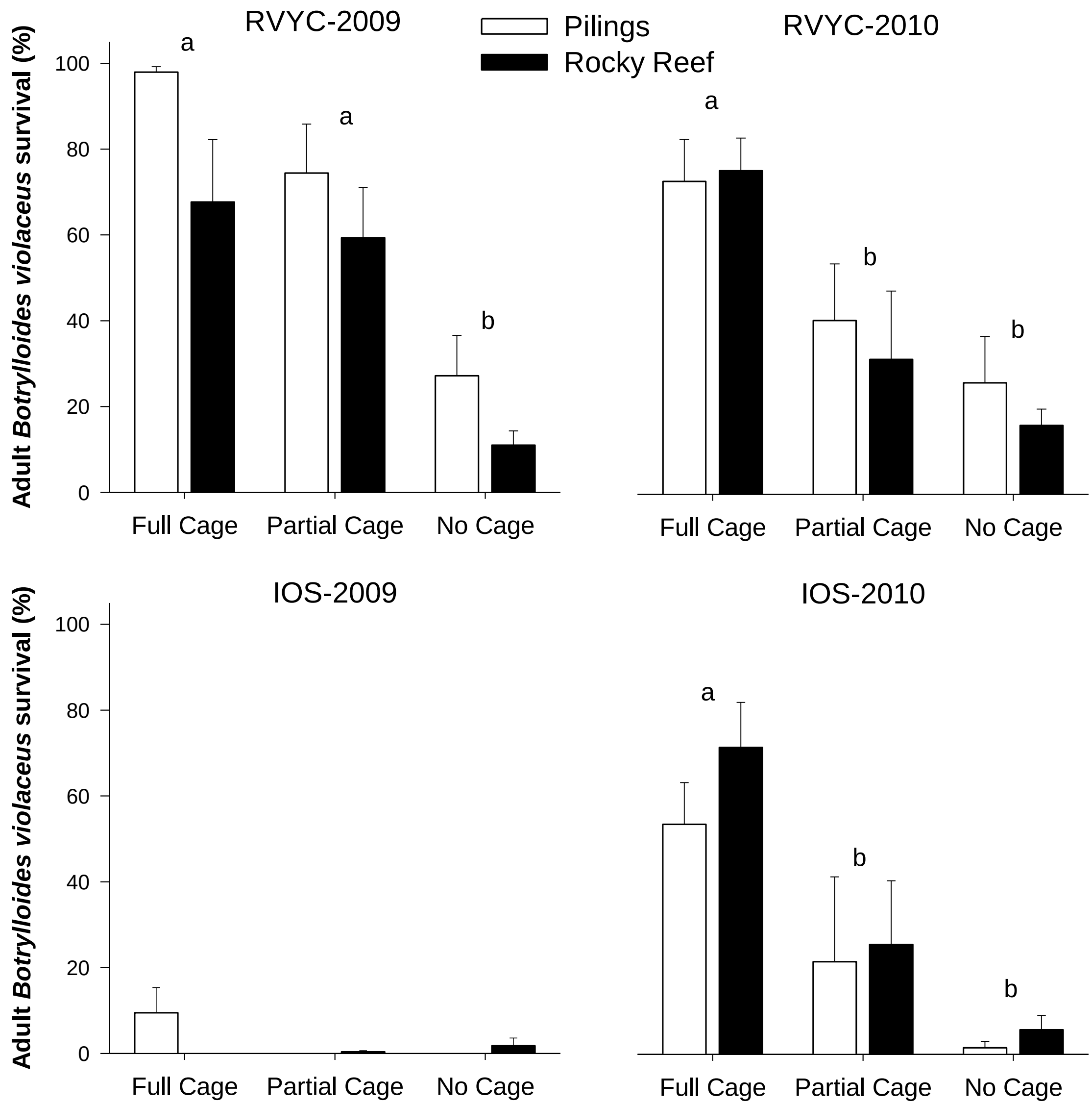

Figure 5.1: The percent cover of adult *Botrylloides violaceus* surviving per treatment (full cage, partial cage, and no cage) at the end of the three-week exclusion experiments in 2009 and 2010. Experiments were run in two habitat types (marina pilings and subtidal rocky reef) per location (Royal Victoria Yacht Club-RVYC and Institute of Ocean Sciences-IOS). Significant differences between treatment means ($p<0.01$) are denoted by different letters above bars (Tukey's HSD test).

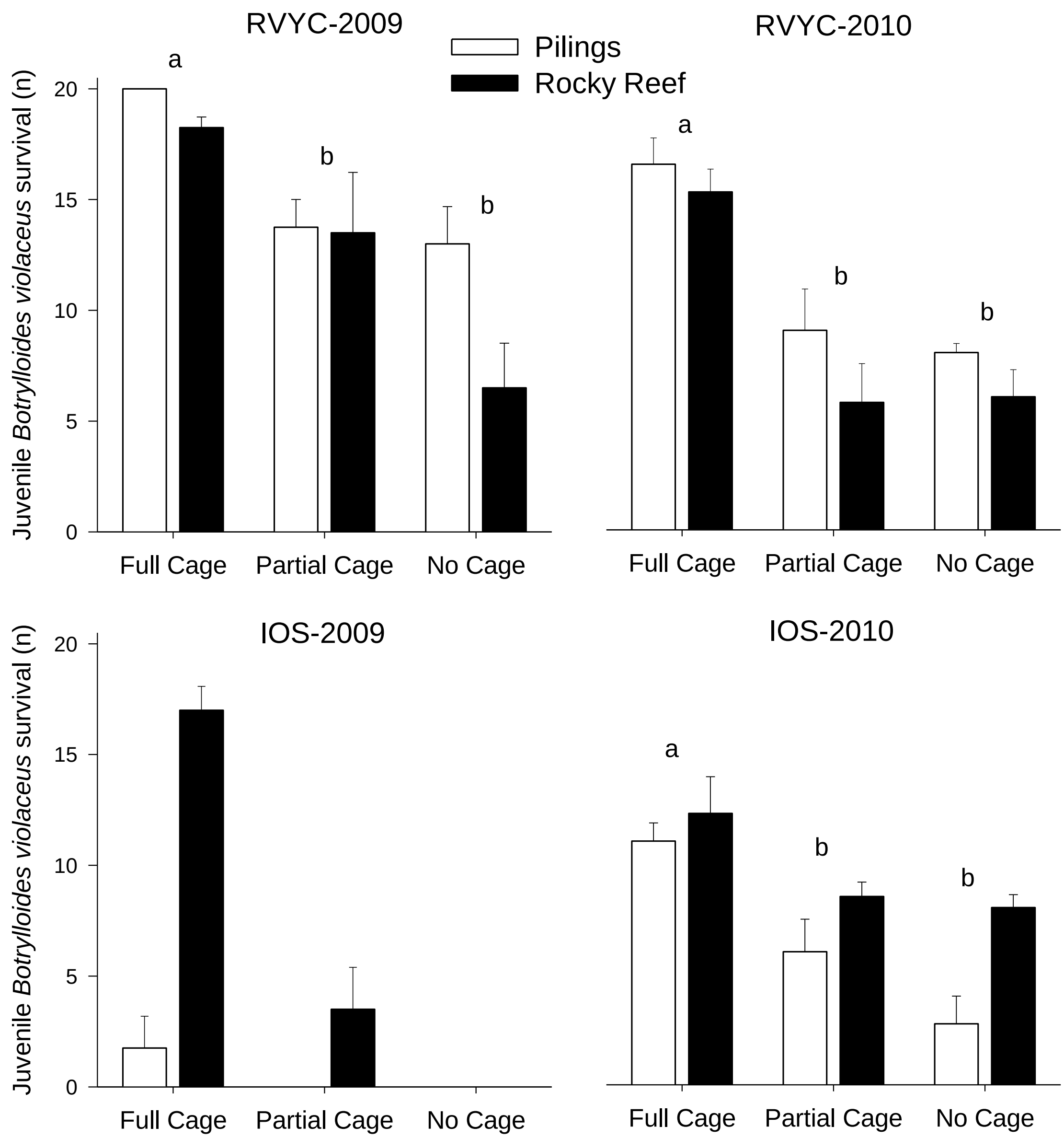

Figure 5.2: Number of juvenile *Botrylloides violaceus* surviving per treatment (full cage, partial cage, and no cage) at the end of the three-week exclusion experiments in 2009 and 2010. Juvenile colonies were < 1 week old at time of deployment and experiments were run in two habitat types (marina pilings and subtidal rocky reef) per location (Royal Victoria Yacht Club-RVYC and Institute of Ocean Sciences-IOS). Significant differences between treatment means ($p<0.01$) are denoted by different letters above bars (Tukey's HSD test).

Table 5.2: Two-way (habitat, life stage) ANOVAs for survival in juvenile and adult *Botrylloides violaceus*. Data from 2010 IOS was analyzed with a non-parametric Scheirer-Ray-Hare test. Bold values indicate statistical significance (P <0.01).

	df	SS	F	*P*
2009 RVYC				
Habitat	1	2411.70	8.84	**0.012**
Lifestage	1	3466.00	12.71	**0.004**
Habitat * Life stage	1	252.50	0.93	0.355
Transformation	none			
2010 RVYC				
Habitat	1	327.68	2.97	0.110
Lifestage	1	386.50	3.51	0.086
Habitat * Life stage	1	1.19	0.01	0.919
Transformation	reflected, Arcsine Sqrt			
2010 IOS				
Habitat	1	17.72	1.33	0.270
Lifestage	1	52.54	3.96	0.070
Habitat * Life stage	1	17.72	1.33	0.270
Transformation	none			

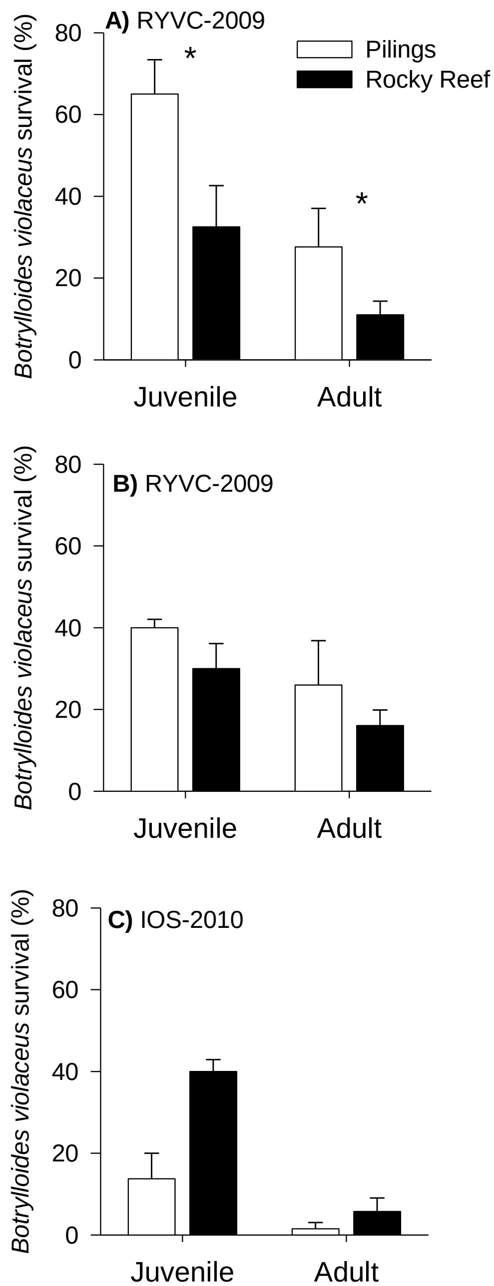

Figure 5.3: Percent survival of adult and juvenile *Botrylloides violaceus* in experimental uncaged treatments. Data are from field experiments run in piling and rocky reef habitat at the Royal Victoria Yacht Club (RVYC) during 2009 (A) and 2010 (B) and the Institute of Ocean Sciences (IOS) during 2010 (C). Significant differences between adult and juvenile survival are denoted by asterisks (* P < 0.01).

5.4.2 Observations of potential predators

A high number and diversity of potential predators, including crabs, sea stars, fish, nudibranchs, and flatworms were observed on or around the experimental treatments (Figure 5.4). In 2009, a number of potential predators were observed within the predator exclusion cages of 1 cm x 1 cm mesh, including: the nudibranchs *Dirona albolineata* MacFarland,1905, *Flabellina trophina* (Bergh, 1890), *Geitodoris heathi* (MacFarland, 1905), *Hermissenda crassicornis* (Eschscholtz, 1831), and *Onchidoris bilamellata* (Linnaeus, 1767); the shrimp *Pandalus danae*Stimpson, 1857; the gunnel *Apodichthys flavidus* Girard, 1854; and the flatworms *Eurylepta leoparda* Freeman, 1933, *Kaburakia excelsa* Bock, 1925, and *Notoplana* sp. During both sampling years, large mobile invertebrates and fish were also recorded on and around the experimental treatments.

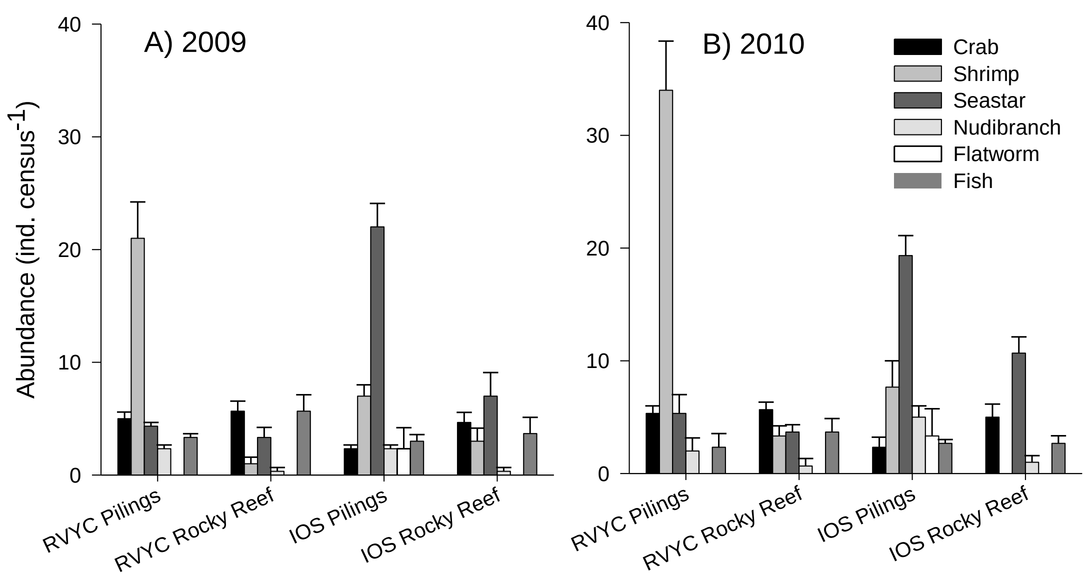

Figure 5.4:Abundance of native benthic predators on pilings and rocky reefs per location (Royal Victoria Yacht Club-RVYC and Institute of Ocean Sciences-IOS) during (A) 2009 and (B) 2010.

The most common potential macro-predators (> 1 cm) included: red rock crab (*Cancer productus* Randall, 1840), sea stars (*Crossaster papposus* (Linnaeus, 1767)), *Dermasterias imbricata* (Grube, 1857), *Evasterias troscheli* (Stimpson, 1862), *Leptasterias hexactis* (Stimpson, 1862), *Pisaster ochraceus* (Brandt, 1835), *Pteraster tesselatus*Ives, 1888, and *Pycnopodia helianthoides* (Brandt, 1835)), and sculpins (e.g. *Artedius harringtoni* (Starks, 1896) and *Artedius lateralis* (Girard, 1854)). Sea urchins (*Strongylocentrotus* spp.) were not observed at the study sites. The dominant benthic predators differed between locations with shrimp being more abundant at RVYC (2009 - $\chi^2 = 30.5$, d.f. = 3, $p < 0.001$; 2010 - $\chi^2 = 63.96$, d.f. = 3, $p < 0.001$) and seastars (2009 - $\chi^2 = 36.67$, d.f. = 3, $p < 0.001$; 2010 - $\chi^2 = 15.3$, d.f. = 3, $p < 0.005$) and flatworms (only seen at IOS) being more abundant at IOS (Figure 5.4). There were no differences in the numbers of crabs, nudibranchs or fish seen at RVYC and IOS.

5.5 Discussion

Anthropogenic habitats play an important role in marine invasions by interacting with human-mediated vectors (Ruiz et al. 2009) and promoting conditions that can enhance the presence of nonindigenous species (NIS) (Floerl et al. 2004; Tyrell and Byers, 2007; Dafforn et al. 2009). In B.C., the invasive colonial ascidian *B. violaceus* is especially prevalent in floating man-made habitats (Gartner 2010, Simkanin et al. 2012), and the findings show that predation by native species can limit the spread of this ascidian to nearby dock pilings and rocky reefs. Furthermore, native benthic predators consumed juvenile and adult ascidian colonies indicating that both life stages are susceptible to predation within the habitats investigated.

Result showed that predators can reduce the survival of *B. violaceus* on dock pilings, however surveys at one of the sites (Royal Victoria Yacht Club) showed that established colonies were present on pilings. It is possible that although predation can limit the survival of ascidians on pilings, their proximity to established colonies on floating docks ensures high propagule delivery, potentially overwhelming biotic resistance. Another possibility is that benthic predators prey on colonies closest to the benthos, creating a depth gradient in the distribution and abundance of *B. violaceus*. Although not quantitatively measured, established *B. violaceus* colonies observed on pilings at RVYC were often closer to the water surface than to the benthos (Simkanin C., personal observation). High recruitment and the varied presence of predators through depth along pilings may reduce predation pressure, allowing some colonies to establish and survive in this habitat type.

A number of potential predators, including crabs, sea stars, fish, nudibranchs, and flatworms were observed during field experiments. At both locations, more benthic predators were recorded in piling communities compared to communities on rocky reefs, which contrasts with previous work suggesting that mobile species abundance may be higher in natural settings (Chapman, 2003; Dumont et al. 2011b). A higher abundance of benthic predators around man-made pilings may be a real pattern in this system; however it is possible that the sampling methodology influenced this result. Observations were made by divers during weekly monitoring of the experimental trials. Around pilings, the habitat was largely homogeneous with pillars surrounded by sandy muddy substrate and very little algae due to overhead shading from dock floats. In these habitats, mobile benthic predators were easy to detect and count. Whereas on rocky reefs, which were more heterogeneous with crevices and large areas of kelp beds, observing potential predators near experimental treatments was more difficult. Also, highly mobile species like crabs, shrimp and seastars may have escaped beneath the algal canopy while divers neared experimental treatments.

Predation is recognized as a significant factor causing post-settlement mortality in newly settled sessile invertebrates (Gosselin and Qian, 1997; Hunt and Scheibling, 1997). In some cases, predation on ascidian recruits is greater than on adults of the same species (Osman and Whitlatch, 1996a). The results showed, however, that juveniles and adults were equally vulnerable to predation, at least over a short temporal window (i.e., three weeks). This is in contrast to results from the East Coast of North America, where predators exhibit weak pressure on *B. violaceus* colonies greater than one week old (Osman and Whitlatch, 1995, 1996a). These varying results may be due to the types of predators acting on the two different coasts. In Connecticut, where predation experiments have been conducted, the dominant predators are believed to be small gastropods (e.g. *Astyris lunata* (Say, 1826) and *Cotonopsis lafresnayi* (P. Fischer and Bernardi, 1856); Whitlatch and Osman, 2009) whereas in B.C. it appears as though generalist benthic predators, such as the sea star *Dermasterias imbricate*, may be predating on *B. violaceus* colonies (Epelbaum et al. 2009c).

In laboratory trials, Epelbaum et al. (2009c) showed that the native urchin *Strongylocentrotus droebachiensis* (O.F. Müller, 1776) consumed juvenile (one week old) and adult *B. violaceus* while the native urchin *Mesocentrotus franciscanus* (A. Agassiz, 1863), the sea star *Dermasterias imbricate*, and the nudibranch *Hermissenda crassicornis* consumed adult *B. violaceus*. However, during trials with a preferred prey item, such as clams or hydroids, none of the four predators preferentially consumed *B. violaceus* (Epelbaum et al. 2009c). It is possible though, that generalist predators, like omnivorous sea stars, act differently in a field setting. Research conducted in nearby Puget Sound, Washington showed that although some sea star predators exhibited prey preferences in the lab, they showed wide variation in their diet in the field (Mauzey et al. 1968). Furthermore, field observations indicate that prey choice is often determined by the relative abundance of a prey species in a particular habitat (Mauzey et al. 1968; Vance and Schmitt, 1979; Annett and Pierotti, 1984). As *B. violaceus* becomes increasing abundant in anthropogenic habitats, such as on dock pilings, native benthic predators may adapt to its presence and increasingly begin to feed on it (as in Carlsson et al. 2009). Predator adaptation to hyper-successful NIS may influence the longer-term dynamics of an invasion by providing resistance to invasions after the initial establishment of a species (Carlsson and Strayer, 2009; Carlsson et al. 2009).

While this study showed that predation may limit the localized spread of *B. violaceus* in B.C., mortality in uncaged treatments was rarely 100%, suggesting that predation may not completely exclude *B. violaceus* from natural rocky reefs. It is possible that some individuals might escape predation, survive to become reproductive, and propagate. Furthermore, habitat selection may alleviate the effect of predation on the distribution and abundance of *B. violaceus* in natural habitats. During SCUBA surveys in 2008, in the few instances where *B. violaceus* was present on rocky reefs, it was found as an epibiont on algae – particularly on fronds of the nonindigenous algae *Sargassum muticum* (Yendo) Yensholt, 1955 (Simkanin C., unpublished results). The presence of *B. violaceus* on *S. muticum* was also noted in eel grass beds on the West Coast of Vancouver Island (White and Orr, 2011). Predation intensity can be lower in vegetation where invertebrates can settle above the benthos (Pohle et al. 1991; Hunt and Scheibling, 1997) and the propensity for *B. violaceus* to settle and survive on the fronds of algae may provide protection from predators. Understanding how predation interacts with other factors will help further determine the likelihood of *B. violaceus* successfully infiltrating and establishing in natural benthic habitats.

Although not tested here, other factors may restrict the localized spread (10^0 – 10^2 m) of *B. violaceus*. For instance, larval dispersal and therefore propagule pressure to natural habitats may be low. Larvae of *B. violaceus* are present in the water column for only minutes to hours (Saito et al. 1981) thus limiting their ability to disperse over great distances. Furthermore, both marinas used for experiments were partially enclosed by breakwaters which can reduce water circulation around marina structures (Floerl and Inglis, 2003), potentially restricting larval dispersal. If larvae do disperse beyond the marina, however, results show that newly settled juveniles are vulnerable to predation. In addition, settlers may face other biotic challenges, such as competition. In natural environments, which often have higher species diversity and therefore increased competition for available space, newer settlers may be less likely to gain a foothold (Lambert, 2005; Dafforn et al. 2012).

B. violaceus was present on dock floats at the two marinas suggesting there might be limited biotic interference to the settlement and survival of this ascidian in floating habitats. Lending further evidence to this idea, Grey (2010) conducted predator exclusion experiments on floating docks in nearby Puget Sound, Washington and found that the recruitment and abundance of *B. violaceus* was not affected by predators in this habitat. The potential for floating structures to offer a spatial refuge from predation has been reported from other parts of the world as well. A recent study in Chile found that by fouling floating aquaculture installations the solitary non-native ascidian *Ciona* *intestinalis* (Linnaeus, 1767) escapes predation pressure from native benthic species (Dumont et al. 2011a). The authors suggest that floating environments may be areas where introduced species can settle, adapt, and continuously generate large numbers of propagules, increasing the likelihood of successful spread to nearby habitats – termed the Persistent Pressure scenario (Dumont et al. 2011a).

The ability of nonindigenous ascidians to gain a foothold in new environments by utilizing floating structures where predation pressure may be limited and free space is readily available has important management implications for the spread of sessile NIS. Floating structures interact directly with human-mediated vectors of NIS, such as recreational boats (Davidson et al. 2010; Clarke Murray et al. 2011), which may increase the likelihood of an invader spreading from one anthropogenic habitat to another (i.e. stepping-stone spread, Glasby and Connell, 1999). Secondly, because recreational boats and commercial vessels are floating, it is probable that species able to survive transport on the bottoms of boats are better adapted to 'jump ship', settle and establish in floating habitats. Finally, as invaders increase in abundance on floating structures, they will release increasing numbers of propagules into surrounding environments, subsequently increasing the likelihood that propagules will escape marina environments. Eradication efforts should be targeted at floating populations – removing large propagule sources and reducing the likelihood of subsequent spread via anthropogenic and natural dispersal.

5.5.1 Conclusions

The results suggest that biotic resistance, through native benthic species preying on both juveniles and adults, plays a role in suppressing the localized spread of *B. violaceus*. Predation by native species may therefore provide resistance to the spread of other high profile globally introduced ascidian species, such as *Botryllus schlosseri*, *Didemnum vexillum* and *Styela clava*, which were also consumed by multiple native species in laboratory trials (Epelbaum et al. 2009c). As *B. violaceus* becomes increasingly abundant on floating structures it is more likely that propagules will escape marina systems, overcome the resistance imposed by potential predators and successfully infiltrate natural benthic systems. The likelihood of arriving propagules overcoming biotic resistance may be especially true in disturbed systems where predation pressure is limited due to habitat destruction, climate induced changes, or overharvesting. Despite both the amount of infrastructure added to coastal environments (Glasby and Connell, 1999; Bulleri and Chapman, 2010) and the number of marine invasions continuing to increase (Ruiz et al. 2000), few studies have begun to investigate how these interacting factors affect natural benthic ecosystems. This study is a step towards better understanding the connection between anthropogenic and natural habitats and which factors are important for mediating invasion dynamics in benthic systems.

Chapter 6: General Discussion

6.1 Summary and Synthesis

The aim of this thesis was to investigate the connection between anthropogenic and natural habitats with respect to the establishment and spread of benthic marine invertebrate invaders. To investigate these questions I conducted a series of desk-based, field-based, and experimental studies. Specifically, I examined global patterns of marine invasions (Chapter 2), local patterns of ascidian invasions (Chapter 3), and used these patterns to inform the design of experimental manipulations to test how factors such as initial inoculation size (Chapter 4) and release from predators (Chapter 5) affect invasion success. My research showed that artificial structures are hubs for sessile marine invasions and may act as focal points for the establishment, growth and spread of nonindigenous populations, especially since they can act as launching points for infiltration of natural habitats. However, species interactions, specifically predation by native species, can meidate the localized spread (or infiltration) of NIS beyond anthropogenic habitats.

Although the distribution and abundance of marine nonindigenous species (NIS) has been studied around the globe (Coles et al. 1999; Ruiz et al. 2000; Hewitt et al. 2004; Galil, 2008), few studies have spanned broad geographical areas and taxonomic groups. A literature review of global scope showed that anthropogenic habitats are indeed centers of marine invasions, but that the prevalence of this pattern varies by organism type (Chapter 2). For example, nonindigenous algal species and mobile invertebrates are often reported from natural habitats, but sessile NIS are known predominately from anthropogenic habitats. These patterns likely reflect the different habitat associations of these species, but may also be influenced by the choice of sampling locations by researchers. Because anthropogenic habitats are readily accessible, they are often targeted for research on marine NIS (Campbell et al. 2007). This is especially true for sessile marine species which settle on hard substrates. Of the 270 studies investigated, only 12% sampled both anthropogenic and natural habitats, and this research was often limited to surveys for just one or two species.

The lack of systematic surveys across habitat types has hindered our understanding of habitat invasibility in marine systems (Ruiz et al. 2009). I addressed this deficiency on a small scale by conducting subtidal surveys across both anthropogenic and natural habitats (Chapter 3). I found that nonindigenous ascidians were largely restricted to artificial structures on Southern Vancouver Island and that this pattern is consistent across their global introduced ranges. Two of the four nonindigenous ascidian species targeted, *Botrylloides violaceus* and *Botryllus schlosseri*, have infiltrated natural habitats in coastal British Columbia (B.C.), but only in low abundances. Thus, my results demonstrate that *in-situ* sampling of both habitat types provides critical information about the distributions of NIS.

Propagule pressure, or the number and frequency of individuals supplied to a new region, is believed to play a critical role in determining the successful establishment of NIS (Lockwood et al. 2005; Simberloff 2009). For many marine species, the period between propagule (or larval) release and recruitment to the adult population is also an important determinant of invasion success - especially for sessile invertebrates (Gosselin and Qian, 1997). I experimentally manipulated propagule pressure in a field setting and showed that post-settlement mortality in *B. violaceus* was high and that large numbers of larvae or frequent introduction events may be needed for successful initial invasion and successful infiltration of natural habitats (Chapter 4). Recruitment varied among floating and fixed habitat types with predation appearing to be one factor responsible for this pattern. This work represents the first study to successfully utilize *in-situ* inoculation techniques to introduce ascidian larvae into field mesocosms and this suggests that such methods can be extended to test a wide variety of hypotheses. These hypotheses could be applied to invasion questions, such as testing the relationship between propagule number and frequency in establishment success, or could target biological questions such as testing how larval size or genetics may affect colonization success.

I conducted field experiments to investigate how predators affected the survival of juvenile and adult *B. violaceus* colonies in anthropogenic (dock pilings) and natural (subtidal rocky reefs) habitats (Chapter 5). My results showed that predators reduced the survival of both life stages in the two habitat types. This highlights the role that biotic resistance can play in suppressing the spread of marine invaders. Predation on NIS by native species may therefore provide some resistance to infiltration by other invasive ascidian species, but this remains to be tested in the field.

6.2 Management Implications

Understanding the factors that affect the distribution and spread of NIS is essential for predicting, preventing, and managing the potential impacts of invasive species (Mack et al. 2000; Hulme, 2006). The prevalence of NIS in man-made habitats (i.e. 63% of the species reviewed in Chapter 2 were reported from such structures) indicates that these sites are focal points for establishment and may facilitate the persistence and spread of invaders. Human-mediated vectors of invasions, such as recreational boating (Floerl and Inglis, 2005; Davidson et al. 2010; Clarke-Murray et al. 2011), directly interact with anthropogenic habitats and therefore are often the first areas colonized by arriving propagules. As such, resource managers should view such sites as crucial 'early warning' locations for monitoring and consider developing rapid response plans for these newly arriving species.

Assuming that most anthropogenic habitats, such as marinas and docks, hold little conservation value, one could argue that if NIS are not spreading to natural habitats their invasion is somewhat inconsequential. Nonetheless, as hubs for invasions such sites may play an important role in the establishment and subsequent spread of invaders. As NIS colonize anthropogenic habitats, they may spread relatively quickly from one artificial structure to another through interaction with human-mediated vectors (e.g. the stepping-stone spread of invaders; Johannesson and Warmos, 1990; Bulleri and Airoldi, 2005; Bulleri and Chapman, 2010). Furthermore, once established, introduced populations may breach barriers to natural dispersal, thereby providing ongoing propagule pressure to nearby habitats and increasing the likelihood of successful infiltration. Thus, artificial habitats such as the underwater structures of marinas, may act as ‘proving grounds’ for invaders upon initial introduction, but also as ‘beachheads’ for greater geographical spread to other marinas and surrounding habitats. Thus, eradication efforts that target newly arrived species on artificial structures should not be viewed simply as conservation strategies for the artificial structure *per se* (although the possibility of infrastructure damage is real in some cases) but as a potential intervention for downstream protection for natural habitats. In this sense, artificial habitats thus provide an initial ‘concentrate and contain’ scenario that is ideally suited to control or eradication strategies before the problem deepens after the invading species has spread into habitats that may not be as readily managed.

Predictive modeling of NIS can provide critical information to identify areas at risk for invasions and inform management responses by governments and conservation agencies (Peterson 2003; Herborg et al. 2009; de Rivera et al. 2011). However, such models are often based on coarse environmental tolerances spanning large geographical scales and often fail to take habitat suitability and/or species interactions into account. In B.C., environmental suitability models for two of the ascidian species currently found in natural habitats (*B. violaceus* and *B. schlosseri*) show that they have the potential to spread throughout the province (Epelbaum et al. 2009a). However, to accurately predict species establishment and spread into natural habitats, data from this thesis (e.g. the habitat distribution of NIS) should be combined with local environmental suitability data. This would serve to increase the predictive power of these models and therefore allow for more targeted management of sensitive habitats. Further this would allow for more efficient resource allocation as targeted management would preclude the need to conduct all activities everywhere.

6.3 Looking Ahead – Future Research Directions

The results presented in this thesis suggest a variety of directions for future research. For instance, it is not yet known whether there are inherent qualities of anthropogenic habitats which make them highly invasible, or whether the presence of NIS in these habitats is largely due to the abundance of human-mediated vectors (i.e. and thus high NIS propagule pressure). It seems likely that both factors play an important role and testing this relationship will be difficult because anthropogenic habitats and vectors of NIS often go hand in hand. British Columbia offers a rare opportunity in this regard, however, because there are numerous Provincial Marine Parks that are frequently visited by recreational boats, but which have limited amounts of artificial structure. It would be interesting to conduct subtidal surveys in these parks to determine the extent to which NIS have invaded natural assemblages of species on rocky reefs in the absence of anthropogenic habitats. This could be partnered with a survey of species on arriving boat hulls (similar to Clarke-Murray et al. 2011) and an assessment of the frequency of boat arrivals (data collected by the B.C. Ministry of Environment, Doug Biffard personal communication). In addition, experimental floating docks that do not receive vessel traffic could be established at varying distances from existing marinas to help tease out the effect of structure absent of the vector.

In order for an invading species to spread beyond its initial introduction location it needs to overcome barriers to its dispersal (Blackburn et al. 2010). Because ascidians have short larval durations (from minutes to hours, Millar 1971; Svane and Young, 1989) it is often assumed that their ability to disperse over great distances is limited (Lambert, 2005; Shanks, 2009) and that this limited dispersal thereby reduces their successful infiltration of nearby natural habitats. However, field observations of ascidians have shown that while most larvae settle quickly, often nearby conspecific adults (Peterson and Svane, 1995; Rius et al. 2010), some do swim up into the water column and may be dispersed over greater distances (> 250 m) (Olson, 1985; Fletcher et al. 2013). It would thus be very informative to conduct dispersal experiments to examine the potential for nonindigenous ascidian larvae to escape marina boundaries. This would help to quantify (i) differences in larval spread capacity among species of interest, (ii) whether initial infiltration success is limited by subsequent natural dispersal, and (iii) whether population size thresholds on marinas must be met prior to successful spread into natural habitats (i.e. thereby overcoming Allee effects).

6.4 Conclusions

Habitat modification and introduced species are considered important threats to native biodiversity (Wilcove et al. 1998; Didham et al. 2007). As coastal ecosystems become increasingly urbanized (and potentially homogenized), artificial structures will continue to be added to the marine environment (Connell and Glasby 1999; Bulleri and Chapman, 2010). These habitats function differently compared to natural habitats and often have different assemblages of species (Connell 2001; Chapman 2003; Bulleri and Chapman, 2010). My research shows that anthropogenic habitats act as reservoirs for marine NIS and may provide beachheads for their infiltration of nearby natural sites. As invaders continue to successfully establish and propagate on man-made structures, the likelihood that their propagules will spread beyond these environments and settle, recruit, and survive in surrounding natural habitats increases. Species interactions, specifically predation by native species, may mediate the localized spread (or infiltration) of NIS beyond anthropogenic habitats, but it is unlikely that predators will completely exclude invaders and managers should be cautious of relying on this to limit the impacts of invasions.

Biological invasions play a key role in changes to species distributions in the ocean and are likely to dominate research agendas for years to come. While the number of marine invasions continues to increase (Ruiz et al. 2000; Ruiz et al. 2011), few studies have begun to investigate the connection between anthropogenic and natural habitats in regards to the spread of NIS. Investigations of natural habitat infiltration by NIS are rare for most marine taxa. Determining the extent to which marine invaders have infiltrated natural benthic habitats is crucial to detecting potential impacts of these species and protecting native ecosystems. Since infiltration success can be expected to vary among taxa and regions habitat-explicit modeling and management will therefore be required to make invasion ecology more predictive and allow for better targeting of management resources.

Bibliography

Abbott, D.P., Johnson, J.V. (1972) The ascidians *Styela barnharti*, *S. plicata*, and *S. montereyensis* in Californian waters. Bulletin of the Southern California Academy of Sciences 71: 95-105.

Airoldi, L. (2003) The effects of sedimentation on rocky coast assemblages. Oceanography and Marine Biology: an Annual Review 41: 161-236.

Airoldi, L., Abbiati, M., Beck, M., Hawkins, S., Jonsson, P., Martin, D., Moschella, P., Sundelöf, A., Thompson, R., Åberg, P. (2005) An ecological perspective on the development and design of low-crested and other hard coastal defense structures. Coastal Engineering, 52: 1073-1087

Airoldi, L., Connell, S., Beck, M. (2009) The loss of natural habitats and the addition of artificial substrata. In: Wahl, W (ed) Marine Hard Bottom Communities: patterns, dynamics, diversity and change. Springer Series: Ecological Studies, Vol. 206, pp 269-280.

Altman, S., Whitlatch, R.B. (2007) Effects of small-scale disturbance on invasion success in marine communities. Journal of Experimental Marine Biology and Ecology 342: 15-29.

Annett, C., Pierotti, R., (1984) Foraging behavior and prey selection of the leather seastar *Dermasterias imbricate*. Marine Ecology Progress Series 14: 197-206.

Apte, S., Holland, B.S., Godwin, L.S., Gardner, J.P.A. (2000) Jumping ship: a stepping stone event mediating transfer of a nonindigenous species via a potentially unsuitable environment. Biological Invasions 2: 75-79.

Arenas, F., Bishop, J.D.D., Carlton, J.T., Dyrynda, P.J., Farnham, W.F., Gonzalez, D.J., Jacobs, M.W., Lambert, C., Lambert, G., Nielsen, S.E., Pederson, J.A., Porter, J.S., Ward, S., Wood, C.A. (2006) Alien species and other notable records from a rapid assessment survey of marinas on the south coast of England. Journal of the Marine Biological Association of the United Kingdom 86: 1329-1338.

Ashton, G.V., Boos, K., Shucksmith, R., Cook, E. (2006) Rapid assessment of the distribution of marine non-native species in marinas in Scotland. Aquatic Invasions 1(4): 209-213

Ban, N., Alder, J. (2008) How wild is the ocean? Assessing the intensity of anthropogenic marine activities in British Columbia, Canada. Aquatic Conservation: Marine and Freshwater Ecosystems 18: 55-85.

Benedetti-Cecchi, L., Chato Osio, G. (2007) Replication and mitigation of effects of confounding variables in environmental impact assessment: effect of marinas on rocky-shore assemblages. Marine Ecology Progress Series 334: 21-35.

Berman, J., Harris, L., Lambert, W., Buttrick, M., Dufresne, M. (1992) Recent invasions of the Gulf of Maine: three contrasting ecological histories. Conservation Biology 6(3): 435-441.

Berrill, N.J. (1950) The Tunicata with an account of the British species. The Ray Society, London.

Blackburn, T.M. (2008) Using aliens to explore how our planet works. Proceedings of the National Academy of Sciences 105(1): 9-10.

Blackburn, T.M., Pyšek, P., Bacher, S., Carlton, J.T., Duncan, R.P., Jarošik, V., Wilson, J.R.U., Richardson, D.M. (2011) A proposed unified framework for biological invasions. Trends in Ecology and Evolution 26(7): 333-339.

Blockley, D., Chapman, M.G. (2006) Recruitment determines differences between assemblages on shaded or unshaded seawalls. Marine Ecology Progress Series 327: 27-36.

Blum, J.C., Chang, A.L., Liljesthröm, M., Schenk, M.E., Steinberg, M.K., Ruiz, G.M. (2007) The non-native solitary ascidian *Ciona intestinalis* (L.) depresses species richness. Journal of Experimental Marine Biology and Ecology 342: 5-14.

Bock, D.G., Zhan, A., Lejeusne, C., MacIsaac, H.J., Cristescu, M.E. (2011) Looking at both sides of the invasion: patterns of colonization in the violet tunicate *Botryllodies violaceus*. Molecular Ecology 20: 503-516.

Briggs, J.C. (2010) Marine biology: the role of accommodation in shaping marine biodiversity. Marine Biology 157: 2117-2126.

Britton-Simmons, K.H., Abbott, K.C. (2008) Short- and long-term effects of disturbance and propagule pressure on a biological invasion. Journal of Ecology 96: 68-77.

Bullard, S., Lambert, G., Carman, M., Byrnes, J., Whitlatch, R., Ruiz, G., Miller, R., Harris, L., Valentine, P., Collie, J., Pederson, J., McNaught, D., Cohen, A., Asch, R., Dijkstra, D., Heinonen, K. (2007) The colonial ascidian *Didemnum* sp. A: Current distribution, basic biology and potential threat to marine communities of the northeast and west coasts of North America. Journal of Experimental Marine Biology and Ecology 342: 99-108.

Bulleri, F, Airoldi, L. (2005) Artificial marine structures facilitate the spread of nonindigenous green alga, *Codium fragile* spp. *tomentosoides*, in the north Adriatic sea. Journal of Applied Ecology 42: 1063-1072.

Bulleri, F., Chapman, M.G. (2004) Intertidal assemblages on artificial and natural habitats in marinas on the north-west coast of Italy. Marine Biology 145: 381-391.

Bulleri, F., Chapman, M.G. (2010) The introduction of coastal infrastructure as a driver of change in marine environments. Journal of Applied Ecology 47: 26-35.

Bulter, A.J., Connolly, R.M. (1996) Development and long term dynamics of a fouling assemblage of sessile marine invertebrates. Biofouling 9: 187-209.

Butler, A.J., Keough, M.J. (1990) A comment on short supply-lines. Trends in Ecology and Evolution 5(3): 97.

Byers, J.E. (2002) Physical habitat attribute mediates biotic resistance to nonindigenous species invasion. Oecologia 130: 146-156.

Byrnes, J.E., Reynolds, P.L., Stachowicz, J.J. (2007) Invasions and extinctions reshape coastal marine food webs. PLoS ONE 2(3): e295. doi:10.1371/journal.pone.000295.

Campbell, M.L., Gould, B., Hewitt, C.L. (2007) Survey evaluations to assess marine bioinvasions. Marine Pollution Bulletin 55: 360-378.

Carlsson, N.O.L., Sarnelle, O., Strayer, D.L. (2009) Native predators and exotic prey – an acquired taste? Frontiers in Ecology and the Environment 10(7): 525-532.

Carlsson, N.O.L., Strayer, D.L. (2009) Intraspecific variation in the consumption of exotic prey – a mechanism that increases biotic resistance against invasive species? Freshwater Biology 54: 2315-2319.

Carlton, J.T. (1979) History, biogeography, and ecology of the introduced marine ad estuarine invertebrates of the Pacific Coast of North America.Ph.D. dissertation, University of California, Davis.

Carlton, J.T. (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanography and Marine Biology Annual Review 23: 313-371.

Carlton, J.T. (1989) Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. Conservation Biology 3(3): 265-273.

Carlton, J.T. (1996a) Biological invasions and cryptogenic species. Ecology 77(6): 1653-1655.

Carlton, J.T. (1996b) Patterns, process, and prediction in marine invasion ecology. Biological Conservation 78: 97-106.

Carlton, J.T., Geller, J.B. (1993) Ecological roulette: the global transport of nonindigenous marine organisms. Science 261(5117): 78-82.

Carlton, J.T., Hodder, J. (1995) Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16th century sailing vessel. Marine Biology 121: 721-730.

Carver, C.E., Chisholm, A., Mallet, A.L. (2003) Strategies to mitigate the impact of *Ciona intestinalis* (L.) biofouling on shellfish production. Journal of Shellfish Research 22(3): 621-631.

Cassey, P., Blackburn, T.M., Sol, D., Duncan, R.P., Lockwood, J.L. (2004) Global patterns of introduction effort and establishment success in birds. Proceedings of the Royal Society of London, Series B (Suppl.) 271: S405-8.

Castilla, J.C., Guiñez, R., Caro, A.U., Ortiz, V. (2004) Invasion of a rocky intertidal shore by the tunicate *Pyura praeputialis* in the Bay of Antofagasta, Chile. Proceedings of the National Academy of Sciences of the USA 101(23): 8517-8524.

Chapman, J.W. (1988) Invasions of the Northeast Pacific by Asian and Atlantic Gammaridean Amphipod Crustaceans, including a new species of *Corophium*. Journal of Crustacean Biology 8(3): 364-382.

Chapman, J.W., Carlton, J.T. (1991) A test of criteria for introduced species: the global invasion by the isopod Synidotea laevidorsalis (Miers, 1881). Journal of Crustacean Biology 11(3): 386-400.

Chapman, M.G. (2003) Paucity of mobile species on constructed seawalls: effects of urbanization on biodiversity. Marine Ecology Progress Series 264: 21-29.

Chapman, M.G., Blockley, D.G. (2009) Engineering novel habitats on urban infrastructure to increase intertidal biodiversity. Oecologia 161: 625-635.

Chapman, M.G., Underwood, A.J. (2011) Evaluation of ecological engineering of "armoured" shorelines to improve their value as habitat. Journal of Experimental Marine Biology and Ecology 400: 302-313.

Chew, M.K. (2011) Invasion biology: historical precedents. Encyclopedia of Biological Invasions (eds. Simberloff, D., Rejmánek, M.)University of California Press.Pages 369-375.

Choi, F.M.P. (2011) Assessing intertidal marine non-indigenous species in Canadian ports.MSc. thesis, University of British Columbia, Canada.

Chytrý, M. Maskell, L.C., Pino, J., Pyšek, P., Vilà, M., Font, X., Smart, S.M. (2008) Habitat invasions by alien plants: a quantitative comparison among Mediterranean, subcontinental and oceanic regions of Europe. Journal of Applied Ecology 45: 448-458.

Cinar, M.E. (2006) Serpulid species (Polychaeta: Serpulidae) from the Levantine coast of Turkey (eastern Mediterranean) with special emphasis on alien species. Aquatic Invasions 1(4): 223-240

Cinar, M.E., Bilecenoglu, M., Ozturk, B., Can, A. (2006) New records of alien species on the Levantine coast of Turkey. Aquatic Invasions 1(2): 84-90

Clark, G.F., Johnston, E.L. (2005) Manipulating larval supply in the field: a controlled study of marine invasibility. Marine Ecology Progress Series 298: 9-19.

Clark, G.F., Johnston, E.L. (2009) Propagule pressure and disturbance interact to overcome biotic resistance to marine invertebrate communities. Oikos 118: 1679-1686.

Clark, G.F., Johnston, E.L. (2011) Temporal change in the diversity-invisibility relationship in the presence of a disturbance regime. Ecology Letters 14: 52-57.

Clarke Murray, C., Pakhomov, E.A., Therriault, T.W. (2011) Recreational boating: a large unregulated vector transporting marine invasive species. Diversity and Distributions 17(6): 1161-1172.

Clarke, C.L., Therriault, T.W. (2007) Biological synopsis of the invasive tunicate *Styela clava* (Herdman 1881). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2807: 23pp.

Clynick, B.G., Blockley, D., Chapman, M.G. (2009) Anthropogenic changes in patterns of diversity on hard substrata: an overview. In: Rilov G, Crooks J (eds) Biological Invasions in Marine Ecosystems. Springer-Verlag, Berlin. pp 247-256.

Clynick, B.G., Chapman, M.G., Underwood, A.J. (2008) Fish assemblages associated with urban structures and natural reefs in Sydney, Australia. Austral Ecology 33: 140-150.

Cohen, A.N. (2005) Guide to the Exotic Species of San Francisco Bay. San Francisco Estuary Institute, Oakland, CA www.exoticsguide.org Consulted on 2011-01-30

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

Cohen, A.N., Harris, L.H., Bingham, B.L., Carlton, J.T., Chapman, J.W., Lambert, C.C., Lambert, G., Ljubenkov, J.C., Murray, S.N., Rao, L.C., Reardon, K., Schwindt, E. (2005) Rapid assessment survey for exotic organisms in southern California bays and harbors, and abundance in port and non-port areas. Biological Invasions 7: 995-1002

Colautti, R.I., Bailey, S.A., van Overdijk, C.D.A., Amundsen, K., MacIsaac, H.J. (2006) Characterised and projected costs of nonindigenous species in Canada. Biological Invasions 8: 45-59.

Colautti, R.I., Grigorovich, I.A., MacIsaac, H.J. (2006) Propagule pressure: a null model for biological invasions. Biological Invasions 8: 1023-1037

Colautti, R.I., MacIsaac, H.J. (2004) A neutral terminology to define 'invasive' species. Diversity and Distributions 10: 135-141.

Colautti, R.I., Ricciardi, A., Grigorovich, I.A., MacIsaac, H.J. (2004) Is invasion success explained by the enemy release hypothesis? Ecology Letters 7: 721-733.

Coles, S.L., DeFelice, R.C., Eldredge, L.G., Carlton, J.T. (1999) Historical and recent introductions of non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian Islands. Marine Biology 135: 147-158.

Connell, J.H. (1985) The consequences of variation in initial settlement vs. post-settlement mortality in rocky intertidal communities. Journal of Experimental Marine Biology and Ecology 93: 11-45.

Connell, J.H., Keough, M.J. (1985) Disturbance and patch dynamics of subtidal marine animals on hard substrata, in: Pickett, S.T.A., White, P.S. (Eds.), The Ecology of Natural Disturbance and Patch Dynamics. Academic Press, Inc., Florida, pp. 125-151.

Connell, S.D. (2000) Floating pontoons create novel habitats for subtidal epibiota. Journal of Experimental Marine Biology and Ecology 247: 183-194.

Connell, S.D. (2001) Urban structures as marine habitats: an experimental comparison of the composition and abundance of subtidal epibiota among pilings, pontoons and rock reefs. Marine Environmental Research 52: 115-125

Connell, S.D., Glasby, T.M. (1999) Do urban structures influence local abundance and diversity of subtidal epibiota? A case study from Sydney Harbour, Australia. Marine Environmental Research 47: 373-387.

Cordell, J.R., Levy, C., Toft, J.D. (2013) Ecological implications of invasive tunicates associated with artificial structures in Puget Sound, Washington, USA. Biological Invasions 15(6): 1303-1318.

Costello, M.J., Coll, M., Danovaro, R., Halpin, P., Ojaveer, H., Miloslavich, P. (2010) A census of marine biodiversity knowledge, resources, and future challenges. PLoS ONE 5(8), e12110. doi:10.1371/journal.pone.0012110.

Coutts, A.D.M., Forrest, B.M. (2007) Development and application of tools for incursion response: lessons learned from the management of the fouling pest *Didemnum vexillum*. Journal of Experimental Marine Biology and Ecology 342: 154-162.

Coutts, A.D.M., Moore, K.M., Hewitt, C. (2003) Ships' sea-chests: an overlooked transfer mechanism for non-indigenous marine species? Marine Pollution Bulletin 46: 1504-1515.

Daehler, C.C. (2006) Invasibility of tropical islands by introduced plants: partitioning the influence of isolation and propagule pressure. Preslia 78: 389-404.

Dafforn, K.A., Glasby, T.M., Johnston, E.L. (2008) Differential effects of tributyltin and copper antifoulants on recruitment of non-indigenous species. Biofouling 24(1): 23-33.

Dafforn, K.A., Glasby, T.M., Johnston, E.L. (2012) Comparing the invisibility of experimental 'reefs' with field observations of natural reefs and artificial structures. PLoS ONE 7(5), e38124.

Dafforn, K.A., Johnston, E.L., Glasby, T.M. (2009) Shallow moving structures promote marine invader dominance. Biofouling 25(3): 277-287.

Daniel, K.S., Therriault, T.W. 2007.Biological synopsis of the invasive tunicate *Didemnnum* sp. Canadian Manuscript Report of Fisheries and Aquatic Sciences. 2788: 53pp.

Darling, J.A., Kuenzi, A., Reitzel, A.M. (2009). Human-mediated transport determines the non-native distribution of the anemone *Nematostella vectensis*, a dispersal-limited estuarine invertebrate. Marine Ecology Progress Series 380: 137-146.

Davidson, I.C., Zabin, C.J., Chang, A.L., Brown, C.W., Sytsma, M.D., Ruiz, G.M. (2010) Recreational boats as potential vectors of marine organisms a an invasion hotspot. Aquatic Biology 11: 179-191.

Davis, A.R. (1987) Effects of variation in initial settlement on distribution and abundance of *Podoclavella moluccensis* Sluiter. Journal of Experimental Marine Biology and Ecology 117: 157-167.

Davis, M.A. (2009) Invasion Biology. Oxford University Press Inc., New York. 244p

Davis, M.A., Grime, J.P., Thompson, K. (2000) Fluctuating resources in plant communities: a general theory of invisibility. Journal of Ecology 88: 528-534.

Dayton, P.K. (1971) Competition, disturbance, and community organization: the provision and subsequent utilization of space in a rocky intertidal community. Ecology Monographs 41(4): 351-389.

de Rivera, C., Ruiz, G.M., Hines, A.H., Jivoff, P. (2005) Biotic resistance to invasion: native predator limits abundance and distribution of an introduced crab. Ecology 86: 3364-3376.

de Rivera, C.E., Steves, B.P., Fofonoff, P.W., Hines, A.H., Ruiz, G.M. (2011) Potential for high-latitude marine invasions along western North America. Diversity and Distributions 17(6): 1198-1209.

Didham, R.K., Tylianakis, J.M., Gemmell, N.J., Rand, T.A., Ewers, R.M. (2007) Interactive effects of habitat modification and species invasion on native species decline. Trends in Ecology and Evolution 22(9): 489-496.

Dijkstra, J., Harris, L.G., Weterman, E. (2007) Distribution and long-term temporal patterns of four invasive colonial ascidians in the Gulf of Maine. Journal of Experimental Marine Biology and Ecology 342: 61-68.

Dijkstra, J.A., Westerman, E.L., Harris, L.G. (2010) The effects of climate change on species composition, succession and phenology: a case study. Global Change Biology 17(7): 2360-2369.

Drake, J.F., Mooney, H.A., di Castri, F., Groves, R.H., Kruger, F.J., Rejmánek, M., Williamson, M. (1989) Biological Invasions: A Global Perspective. John Wiley & Sons, Chichester.

Dumont, C.P., Gaymer, C.F., Theil, M. (2011a) Predation contributes to invasion resistance of benthic communities against the nonindigenous tunicate *Ciona intestinalis*. Biological Invasions 13: 2023-2034.

Dumont, C.P., Harris, L.G., Gaymer, C.F. (2011b) Anthropogenic structures as a spatial refuge from predation for the invasive bryozoan *Bugula neritina*. Marine Ecology Progress Series 427: 95-103.

Eldredge, L. G. (1966) Taxonomic review of Indo-Pacific didemnid ascidians and descriptions of twenty-three central Pacific species. Micronesica 2: 161-261.

Elton, C.S. (1958) The Ecology of Invasions by Animals and Plants. Chapman and Hall, London.

Epelbaum, A. Herborg, L.M., Therriault, T.W., Pearce, C.M. (2009a) Temperature and salinity effects on growth, survival, reproduction, and potential distribution of two non-indigenous botryllid ascidians in British Columbia. Journal of Experimental Marine Biology and Ecology 369: 43-52.

Epelbaum, A., Pearce, C.M., Barker, D.J., Paulson, A., Terriault, T.W. (2009c) Susceptibility of non-indigenous ascidian species in British Columbia (Canada) to invertebrate predation. Marine Biology 156: 1311-1320.

Epelbaum, A., Therriualt, T.W., Paulson, A., Pearce, C.M. (2009b) Botryllid tunicates: culture techniques and experimental procedures. Aquatic Invasions 4(1): 111-120.

Fletcher, L.M., Forrest, B.M., Bell, J.J. (2013) Natural dispersal mechanism and dispersal potential of the invasive ascidian *Didemnum vexillum*. Biological Invasions 15: 627-643.

Floerl, O., Inglis, G. (2003) Boat harbour design can exacerbate hull fouling. Austral Ecology 28: 116-127.

Floerl, O., Inglis, G.J. (2005) Starting the invasion pathway: the interaction between source populations and human transport vectors. Biological Invasions 7: 589-606.

Floerl, O., Inglis, G.J., Dey, K., Smith, A. (2009b) The importance of transport hubs in stepping-stone invasions. Journal of Applied Ecology 46: 37-45.

Floerl, O., Inglis, G.J., Gordon, D.P. (2009a) Patterns of taxonomic diversity and relatedness among native and nonindigenous bryozoans. Diversity and Distributions 15: 438-449.

Floerl, O., Pool, T.K., Inglis, G.J. (2004) Positive interactions between nonindigenous species facilitate transport by human vectors. Ecological Applications 14(6): 1724-1736.

Fofonoff, P.W., Ruiz, G.M., Steves, B., Carlton, J.T. (2003) National Exotic Marine and Estuarine Species Information System. http://invasions.si.edu/nemesis/. Access Date: 28-Mar-2013.

Forsyth, D.M., Duncan, R.P. (2001) Propagule size and the relative success of exotic ungulate and bird introductions to New Zealand. American Naturalist 157: 583-595.

Foster, D.L. (2001) Constraints on colonization and species richness along a grassland productivity gradient: the role of propagule availability. Ecology Letters 4: 530-535.

Galil, B.S. (2008) Alien species in the Mediterranean Sea – which, when, where, why? Hydrobiologia 606: 105-116.

Galil, B.S. (2007) Loss or gain? Invasive aliens and biodiversity in the Mediterranean Sea. Marine Pollution Bulletin 55: 314-322.

Gartner, H. (2010) Subtidal invertebrate fouling communities of the British Columbian coast. MSc. thesis, University of Victoria, B.C., Canada

Geller, J.B., Darling, J.A., Carlton, J.T. (2010) Genetic perspectives on marine biological invasions. Annual Review of Marine Science 2: 367-393.

Gillespie, G.E. (2007) Distribution of non-indigenous intertidal species on the Pacific Coast of Canada. Nippon Suisan Gakkaishi 73(6): 1133-1137.

Gittenberger, A. (2007) Recent population expansions of non-native ascidians in the Netherlands. Journal of Experimental Marine Biology and Ecology 342: 122-126.

Glasby T.M. (1999a) Differences between stubtidal epibiota on pier pilings and rocky reefs at marinas in Sydney, Australia. Estuarine Coastal and Shelf Science 48: 281-290.

Glasby, T.M. (1999b) Effects of shading on subtidal epibiotic assemblages. Journal of Experimental Marine Biology and Ecology 234: 275-290.

Glasby, T.M. (2000) Surface composition and orientation interact to affect subtidal epibiota. Journal of Experimental Marine Biology and Ecology 248: 177-190.

Glasby, T.M., Connell, S.D. (2001) Orientation and position of substrata have large effects on epibiotic assemblages. Marine Ecology Progress Series 214: 127-135.

Glasby, T.M., Connell, S.D. (1999) Urban structures as marine habitat. Ambio 28(7): 595-598.

Glasby, T.M., Connell, S.D., Holloway, M., Hewitt, C. (2007) Nonindigenous biota on anthropogenic structures: could habitat creation facilitate biological invasions? Marine Biology 151: 887-895.

Goldstien S.J., Dupont L., Viard F., Hallas P.J., Nishikawa T., Schiel D.R., Gemmell N.J., Bishop J.D.D. (2011) Global phylogeography of the widely introduced north west pacific ascidian *Styela clava*. PLoS One 6(2): e16755.

Goldstien S.J., Schiel, D.R., Gemmell, N.J. (2010) Regional connectivity and coastal expansion: differentiating pre-border and post-border vectors for the invasive tunicate *Styela clava*. Molecular Ecology 19: 874-885.

Gollasch, S. (2006) Overview on introduced aquatic species in European navigational and adjacent waters. Helgoland Marine Research 60: 84-89.

Gosselin, L.A., Qian, P.Y. (1997) Juvenile mortality in benthic marine invertebrates. Marine Ecology Progress Series 146: 265-282.

Grevstad, F.S. (1999) Experimental invasions using biological control introductions: the influence of release size on the chance of population establishment. Biological Invasions 1: 313-323.

Grey, E.K. (2010) Effects of large enemies on success of exotic species in marine fouling communities of Washington, USA. Marine Ecology Progress Series 411: 89-100.

Grosberg, R.K. (1981) Competitive ability influences habitat choice in marine invertebrates. Nature 290: 700-702.

Grosholz, E. (2002) Ecological and evolutionary consequences of coastal invasions. Trends in Ecology and Evolution 17(1): 22-27.

Grozholz, E., Ruiz, G.M. (1996) Predicting the impacts of introduced marine species: lessons from the multiple invasions of the European green crab. Biological Conservation 78 (1-2): 59-66.

Gruner, D.S. (2005) Biotic resistance to an invasive spider conferred by generalist insectivorous birds on Hawai'i Island. Biological Invasions 7: 541-546.

Hedge, L.H., O'Connor, W.A., Johnston, E.L. (2012) Manipulating the intrinsic parameters of propagule pressure: implications for bio-invasion. Ecosphere 3(6): 1-13.

Herborg, L-M., O'Hara, P., Therriault, T.W. (2009) Forecasting the potential distribution of the invasive tunicate *Didemnum vexillum*. Journal of Applied Ecology 46: 64-72.

Hewitt, C.L., Campbell, M.L., Thresher, R.E., Martin, R.B., Boyd, S., Cohen, B.F., Currie, D.R., Gomon, M.F., Keough, M.J., Lewis, J.A., Lockett, M.M., Mays, N., McArthur, M.A., O'Hara, T.D., Poore, G.C.B., Ross, D.J., Storey, M.J., Watson, J.E., Wilson, R.S. (2004) Introduced and cryptogenic species in Port Phillip Bay, Victoria, Australia. Marine Biology 144(1): 183-202.

Hladyz, S., Åbjörnsson, K., Giller, P.S., Woodward, G. (2011) Impacts of an aggressive riparian invader on community structure and ecosystem functioning in stream food webs. Journal of Applied Ecology 48: 443-452.

Hobbs, R.J., Huenneke, L.F. (1992) Disturbance, diversity and invasion: implications for conservation. Conservation Biology 6(3): 324-337.

Hollebone, A.L., Hay, M.E. (2007) Propagule pressure of an invasive crab overwhelms native biotic resistance. Marine Ecology Progress Series 342: 191-196.

Hughes, T.P., Baird, A.H., Dinsdale, E.A., Moltschaniwskyj, A., Pratchett, M.S., Tanner, J.E., Wilis, B.L. (2000) Supply-side ecology works both ways: the link between benthic adults, fecundity, and larval recruits. Ecology 81(8): 2241-2249.

Hulme, P.E. (2006) Beyond control: wider implications for the management of biological invasions. Journal of Applied Ecology 43: 835-847.

Hulme, P.E. (2011) Addressing the threat to biodiversity from botanic gardens. Trends in Ecology and Evolution 26(4): 168-174.

Hunt, H.L., Scheibling, R.E. (1997) Role of early post-settlement mortality in recruitment of benthic marine invertebrates. Marine Ecology Progress Series 155: 269-301.

Johannesson, K., Warmoes, T. (1990) Rapid colonization of Belgian breakwaters by the direct developer *Littorina saxatillis* (Olivi) (Prosobranchia, Mollusca).Hydrobiologia 193: 99-108.

Johnston, E.L., Piola, R.F., Clark, G.F. (2009) The role of propagule pressure in invasion success. Pages 133-153 in G. Rilov and J. Crooks (eds.) Marine bioinvasions: ecology, conservation, and management perspectives. Springer, Berlin, Germany.

Kelley, A.L., de Rivera, C.E., Buckley, B.A. (2011) Intraspecific variation in thermotolerance and morphology of the invasive European green crab, *Carcinus maenas*, on the west coast of North America. Journal of Experimental Marine Biology and Ecology 409 (1-2): 70-78.

Knott, N.A., Underwood, A.J., Chapman, M.G., Glasby, T.M. (2004) Epibiota on vertical and on horizontal surfaces on natural reefs and on artificial structures. Journal of the Marine Biological Association of the U.K. 84: 1117-1130.

Kolar, C.S., Lodge, D.M. (2001) Progress in invasion biology: predicting invaders. Trends in Ecology and Evolution 16(4): 199-204.

Lafferty, K.D., Kuris, A.M. (1996) Biological control of marine pests. Ecology 77(7): 1989-2000.

Lamb, A., Hanby, B.P. (2005) Marine Life of the Pacific Northwest. Harbour Publishing, B.C., Canada.

Lambert, C., Lambert, G. (1998) Nonindigenous ascidians in southern California harbors and marinas. Marine Biology 130: 675-688.

Lambert, G. (2002) Nonindigenous ascidians in tropical waters. Pacific Science 56(3): 291-298.

Lambert, G. (2003) New records of ascidians from the NE Pacific: a new species of *Tridemnum*, range extension and description of *Aplidiopsis pannosum* (Ritter, 1899), including its larva, and several non-indigenous species. Zoosystema 24: 665-675.

Lambert, G. (2005) Ecology and natural history of the protocordates. Canadian Journal of Zoology 83: 34-50.

Lambert, G. (2007) Invasive sea squirts: a growing global problem. Journal of Experimental Marine Biology and Ecology 342: 3-4.

Lambert, G. (2009) Adventures of a sea squirt sleuth: unraveling the identity of *Didemnum vexillum* a global ascidian invader. Aquatic Invasions 4(1): 5-28.

Lambert, G., Lambert, C. (2003) Persistence and differential distribution of nonindigenous ascidians in harbors of the Southern California Bight. Marine Ecology Progress Series 259: 145-161.

Lambert, G., Sanamyan, K. (2001) *Distaplia alaskensis* sp. Nov. (Ascidiacea, Aplousobranchia) and other new ascidian records from south-central Alaska, with a redescription of *Ascidia columbiana* (Huntsman, 1912). Canadian Journal of Zoology 79: 1766-1781.

Lawton, J.H., Brown, K.C. (1986) The population and community ecology of invading insects. Philosophical Transactions of the Royal Soceity of London B 314: 607-617.

Levine, J.M., Adler, P.B., Yelenik, S.G. (2004) A meta-analysis of biotic resistance to exotic plant invasions. Ecology Letters 7: 975-989.

Levine, J.M., D'Antonio, C.M. (2003) Forecasting biological invasions with increasing international trade. Conservation Biology 17: 322-326.

Levings, C., Kieser, D., Jamieson, G., Dudas, S. (2002) Marine and estuarine alien species in the Strait of Georgia, British Columbia. Alien Invaders of Canada's Waters, Wetlands and Forests (eds. Natel, P., Claudi, R., Muckle-Jeff, E.) Natural Resources of Canada, Canadian Forest Service, Ottawa. Pgs: 111-131.

Lewin, R. (1986) Supply-side ecology. Science 234(4772): 25-27.

Lockwood, J.L., Cassey, P., Blackburn, T. (2005) The role of propagule pressure in explaining species invasions Trends in Ecology and Evolution 20(5): 223-228.

Lockwood, J.L., Cassey, P., Blackburn, T.M. (2009) The more you introduce the more you get: the role of colonization pressure and propagule pressure in invasion ecology. Diversity and Distributions 15: 904-910.

Lockwood, J.L., Hoopes, M.F., Marchetti, M.P. (2007) Invasion Ecology. Blackwell Publishing, Oxford.

Lonsdale, W.M. (1999) Global patterns of plant invasions and the concept of invasibility. Ecology 80(5): 1522-1536.

López-Legentil, S., Turon, X., Planes, S. (2006) Genetic structure of the star sea squirt, *Botryllus schlosseri*, introduced in southern European harbours. Molecular Ecology 15: 3957-3967.

Lozon, J.D., MacIsaac, H.J. (1997) Biological invasions: are they dependent on disturbance? Environmental Reviews 5: 131-144.

Lu, L., Levings, C.D., Piercey, G.E. (2007) Preliminary investigation on aquatic invasive species of marine and estuarine macrobenthic invertebrates on floating structures in five British Columbia harbors. Canadian Manuscript Report of Fisheries and Aquatic Sciences 2814: 30pp.

Lutz-Collins, V., Ramsay, A., Quijón, P.A., Davidson, J. (2009) Invasive tunicates fouling mussel lines: evidence of their impact on native tunicates and other epifaunal invertebrates. Aquatic Invasions 4(1): 213-220.

Lützen, J. (1999) *Styela clava* Herdman (Urochordata, Ascidiacea), a successful immigrant to North West Europe: ecology, propagation and chronology of spread. Helgolander Meeresuntersuchungen 52: 383-391.

Mack, R.N., Simberloff, D., Lonsdale, W.M., Evans, H., Clout, M., Bazzaz, F.A. (2000) Biotic invasions: causes, epidemiology, global consequences, and control. Ecological Applications 10(3): 689-710

Marins, F.O., Novaes, R.L.M., Rocha, R.M., Junqueira, A.O.R. (2010) Non indigenous ascidians in port and natural environments in a tropical Brazilian bay. Zoologia 27(2): 213-221.

Marshall, D.J., Keough, M.J. (2003) Effects of settler size and density on early post-settlement survival of *Ciona intestinalis* in the field. Marine Ecology Progress Series 259: 139-144.

Marshall, D.J., Styan, C.A., Keough, M.J. (2000) Intraspecific co-variation between egg and body size affects fertilization kinetics of free-spawning marine invertebrates. Marine Ecology Progress Series 195: 305-309.

Mauzey, K.P., Birkeland, C., Dayton, P.K. (1968) Feeding behavior of asteroids and escape responses of their prey in the Puget Sound Region. Ecology 49(4): 603-619.

McKindsey, C.W., Landry, T., O'Beirn, F.X., Davies, I.M. (2007) Bivalve aquaculture and exotic species: a review of ecological considerations and management issues. Journal of Shellfish Research 26(2): 281-294.

Millar, R.H. (1971) The biology of Ascidians. Advances in Marine Biology 9: 1-100.

Miller, R.J., Etter, R.J. (2008) Shading facilitates sessile invertebrate dominance in the rocky subtidal Gulf of Maine. Ecology 89(2): 452-62.

Miller, R.J., Ettter, R.J. (2011) Rock walls: small-scale diversity hotspots in the subtidal Gulf of Maine. Marine Ecology Progress Series 425: 153-165.

Mills, E.L., Leach, J.H., Carlton, J.T., Secor, C.L. (1993) Exotic species in the great lakes: a history of biotic crises and anthropogenic introductions. Journal of Great Lakes Research 19(1): 1-54.

Milton, S.J., Wilson, J.R.U., Richardson, D.M., Seymour, C.L., Dean, W.R.J., Iponga, D.M., Proches, S. (2007) Invasive alien plants infiltrate bird-mediated shrub nucleation processes in arid savanna. Journal of Ecology 95: 648-661.

Minchin, D. (2007) Rapid coastal survey for targeted alien species associated with floating pontoons in Ireland. Aquatic Invasions 2(1): 63-70

Mitcheli, F., Peterson, C.H., Mullineaux, L.S., Fisher, C.R., Mills, S.W., Sancho, G. Johnson, G.A., Lenihan, H.S. (2002) Predation structures communities at deep-sea hydrothermal vents. Ecological Monographs 72(3): 365-382.

Monniot, C., Monniot, F., Laboute, P. (1991) Coral reef ascidians of New Caledonia. Orstom, Paris.

Mukai, H., Saito, Y., Watanabe, H. (1987) Viviparous development in *Botrylloides* (compound ascidians). Journal of Morphology 193: 263 -276.

Nandakumar, K., Tanaka, M., Kikuchi. T. (1993) Interspecific competition among fouling organism in Tomioka Bay, Japan. Marine Ecology Progress Series 94: 43-50.

Naylor, R.L., Williams, S.L., Strong, D.R. (2001) Aquaculture – a gateway for exotic species. Science 294: 1655-1656.

Norton, T.A. (1992) Dispersal by macroalgae. British Journal of Phycology 27: 293-301

Olson, R.R. (1985) The consequences of short-distance larval dispersal in a sessile marine invertebrate. Ecology 66: 30-39.

Osman, R.W., Whitlatch, R.B. (1995a) Predation on early ontogenetic life stages and its effect on recruitment into a marine epifaunal community. Marine Ecology Progress Series 117: 111-126.

Osman, R.W., Whitlatch, R.B. (1995b) The influence of resident adults on recruitment: a comparison to settlement. Journal of Experimental Marine Biology and Ecology 190: 169-198.

Osman, R.W., Whitlatch, R.B. (2004) The control of the development of a marine benthic community by predation on recruits. Journal of Experimental Marine Biology and Ecology 311: 117-145.

Osman, R.W., Whitlatch, R.B. (1996) Process affecting newly-settled juveniles and the consequences to subsequent community development. Invertebrate Reproduction and Development 30(1-3): 217-225.

Page, H., Dugan, J., Culver, C., Hoesterey, J. (2006) Exotic invertebrate species on offshore oil platforms. Marine Ecology Progress Series 325: 101-107.

Petersen, J.K., Svane, I. (1995) Larval dispersal in the ascidian *Ciona intestialis* (L.) Evidence for a closed population. Journal of Experimental Marine Biology and Ecology 186: 89-102.

Pimentel, D., Zuniga, R., Morrison, D. (2005) Update on the environmental and economic costs associated with alien-invasive species in the United States. Ecological Economics 52: 273-288.

Piola, R., Johnston, E. (2008) Pollution reduces native diversity and increases invader dominance in marine hard-substrate communities. Diversity and Distributions 14: 329-342.

Pohle, D.G., Bricelj, V.M., García-Esquivel, Z. (1991) The eelgrass canopy: an above-bottom refuge from benthic predators for juvenile bay scallops *Argopecten irradians*. Marine Ecology Progress Series 74: 47-59.

Pomerat, C.M., Reiner, E.R. (1942) The influence of surface angle and of light on attachment of barnacles and other sedentary organisms. The Biological Bulletin 8: 14-25.

Priesler.R., Wasson, K., Wolff, W., Tyrrell, M. (2009) Invasions of estuaries versus the adjacent open coast: a global perspective. In: Rilov G, Crooks J (eds) Biological Invasions in Marine Ecosystems. Springer-Verlag, Berlin. pp 587-617.

Pyšek, P., Richardson, D.M, Jarošík, V. (2006) Who cites who in the invasion zoo: insights from an analysis of the most highly cited papers in invasion ecology. Preslia 78: 437-468.

Pyšek, P., Richardson, D.M., Pergl, J., Jarošík, V., Sixtová, Z., Weber, E. (2008) Geographical and taxonomic biases in invasion ecology. Trends in Ecology and Evolution 23(5): 237-244.

Qian, H., Ricklefs, R.E. (2006) The role of exotic species in homogenizing the North American flora. Ecology Letters 9: 1293-1298.

Quinn, G.P., Keough, M.J., 2002. Experimental Design and Data Analysis for Biologists. Cambridge University Press, New York.

Ramsay, A., Davidson, J., Landry, T., Arsenault, G. (2008) Process of invasiveness among exotic tunicates in Prince Edward Island, Canada. Biological Invasions 10: 1311-1316.

Reed, D.C., Foster, M.S. (1984) The effects of canopy shadings on algal recruitment and growth in a giant kelp forest. Ecology 65(3): 937-948.

Reichard, S.H., White, P. (2001) Horticulture as a pathway of invasive plant introductions in the United States. BioScience 51(2): 103-113.

Reusch, T.B.H., (1998) Native predators contribute to invasion resistance to the nonindigenous bivalve *Musculista senhousia* in southern California, USA. Marine Ecology Progress Series 170: 159-168.

Ricciardi, A. (2006) Patterns of invasion of the Laurentian Great Lakes in relation to changes in vector activity. Diversity and Distributions 12: 425-433.

Richardson, D.M., Pyšek, P. (2008) Fifty years of invasion ecology – the legacy of Charles Elton. Diversity and Distributions 14: 161-168.

Richardson, D.M., Pyšek, P., Rejmánek, M., Barbour, M.G., Panetta, F.D., West, C.J. (2000) Naturalization and invasion of alien plants: concepts and definitions. Diversity and Distributions 6: 93-107.

Rius, M. Branch, G.M., Griffiths, C.L., Turon, X. (2010) Larval settlement behaviour in six gregarious ascidians in relation to adult distribution. Marine Ecology Progress Series 418: 151-163.

Rius, M., Heasman, K.G., McQuaid, C.D. (2011) Long-term coexistence of non-indigenous species in aquaculture facilities. Marine Pollution Bulletin 62: 2395-2403.

Rius, M., Pascual, M., Turon, X. (2008) Phylogeography of the widespread marine invader *Microcosmus squamiger* (Ascidiacea) reveals high genetic diversity of introduced populations and non-independent colonizations. Diversity and Distributions 14: 818-828.

Rius, M., Turon, X., Marshall, D.J. (2009) Non-lethal effects of an invasive species in the marine environment: the importance of early life-history stages. Oecologia 159: 873-882.

Rodriguez, L.F., Ibarra-Obando, S.E. (2008) Cover and colonization of commercial oyster (*Crassostrea gigas*) shells by fouling organisms in San Quintin Bay, Mexico. Journal of Shellfish Research 27: 337-343.

Ruesink, J.L. (2007) Biotic resistance and facilitation of an non-native oyster on rocky shores. Marine Ecology Progress Series 331: 1-9.

Ruiz, G.M., Fofonoff, P.W., Carlton, J.T., Wonham, M.J., Hines, A.H. (2000) Invasion of coastal marine communities in North America: apparent patters, processes and biases. Annual Review of Ecology and Systematics 31: 481-531.

Ruiz, G.M., Fofonoff, P.W., Steves, B., Foss, S.F., Shiba, S.N. (2011) Marine invasion history and vector analysis of California: a hotspot for western North America. Diversity and Distributions 17(2) 362-373.

Ruiz, G.M., Freestone, A., Fofonoff, P., Simkanin, C. (2009) Habitat distribution and heterogeneity in marine invasion dynamics: The importance of hard substrate and anthropogenic structure. In: Wahl, W (ed) Marine Hard Bottom Communities: patterns, dynamics, diversity and change. Springer Series: Ecological Studies, Vol. 206, pp 321-332.

Ruiz, G.M., Hewitt, C.L. (2009) Latitudinal patterns of biological invasions in marine ecosystems: A polar perspective. In: Krupnik, I., Lang, M.A, Miller, S.E. (eds) Smithsonian at the poles: contributions to International Polar Year science, pp 347-358.

Russ, G.R. (1982) Overgrowth in a marine epifaunal community: competitive hierarchies and competitive networks. Oecologia 53: 12-19.

Saito, Y., Mukai, H., Watanabe, H. (1981) Studies on Japanese compound styelid Ascidians II. A new species of the genus *Botrylloide*s and redescription of *B. violaceus* Oka. Publications of the Seto Marine Biological Laboratory 26: 357-368.

Sakai, A.K., Allendorf, F.W., Holt, J.S., Lodge, D.M., Molofsky, J., With, K.A., Baughman, S., Cabin, R.J., Cohen, J.E., Ellstrand, N.C., McCauley, D.E., O'Neil, P., Parker, I.M., Thompson, J.N., Weller, S.G. (2001) The population biology of invasive species. Annual Review of Ecology and Systematics 32: 305-332.

Sax, D.F., Gaines, S.D. (2003) Species diversity: from global decreases to local increases. Trends in Ecology and Evolution 18(11): 561-566.

Sax, D.F., Stachowicz, J.J., Brown, J.H., Bruno, J.F., Dawson, M.N., Gaines, S.D., Grosberg, R.K., Hastings, A., Holt, R.D., Mayfield, M.M., O'Connor, M.I., Rice, W.R. (2007) Ecological and evolutionary insights from species invasions. Trends in Ecology and Evolution 22(9): 465-471.

Schoener, T.W., Spiller, D.A. (1995) Effect of predators and area on invasion: an experiment with island spiders. Science 267(5205): 1811-1813.

Semmens, B.X., Buhle, E.R., Salomon, A.K., Pattengill-Semmens, C.V. (2004) A hotspot of non-native marine fishes: evidence for the aquarium trade as an invasion pathway. Marine Ecology Progress Series 266: 239-244.

Shanks, A.L. (2009) Pelagic larval duration and dispersal distance revisited. Biological Bulletin 216: 373-385.

Shenkar, N., Gittenberger, A., Lambert, G., Rius, M., Da Rocha, M., Swalla, B.J., Turon, X. (2011) World Ascidiacea Database.Available online at http://www.marinespcies.org/ascidiacea.Consulted on 2011-04-12.

Shenkar, N., Loya, Y. (2008) The solitary ascidian *Herdmania momus*: native (Red Sea) versus non-indigenous (Mediterranean) populations. Biological Invasions 10: 1431-1439

Shenkar, N., Swalla, B.J. (2011) Global diversity of Ascidiacea. PLoS ONE 6(6): e20657

Simberloff, D. (2009) The role of propagule pressure in biological invasions. Annual Review of Ecology, Evolution and Systematics 40: 81-102.

Simberloff, D., Martin, J-L., Genovesi, P., Maris, V., Wardle, D.A., Aronson, J., Courchamp, F., Galil, B., García-Berthou, E., Pascal, M., Pyšek, P., Sousa, R., Tabacchi, E., Vilà, M. (2013) Impacts of biological invasions: what's what and the way forward. Trends in Ecology and Evolution 28(1): 58-66.

Simberloff, D.S., Wilson, E.O. (1969) Experimental zoography of Islands: the colonization of empty islands. Ecology 50(2): 278-296.

Simkanin, C., Davidson, I.C., Dower, J.F., Jamieson, G., Therriault, T.W. (2013) Anthropogenic structures and the infiltration of natural benthos by invasive ascidians. Marine Ecology 33: 499-511.

Simoncini, M., Miller, R.J. (2007) Feeding preferences of *Strongylocentrotus droebachiensis* (Echinoidea) for a dominant native ascidian, *Aplidium glabrum*, relative the invasive ascidian *Botrylloides violaceus*. Journal of Experimental Marine Biology and Ecology 342: 93-98.

Spalding, M.D., Fox, H.E., Allen, G.R., Davidson, N., Ferdaña, Z.A., Finlayson, M., Halpern, B.S., Jorge, M.A., Lombana, A., Lourie, S.A., Martin, K.D., McManus, E., Molnar, J., Recchia, C.A. Robertson, J. (2007) Marine ecoregions of the world: a bioregionalization of coastal and shelf areas. BioScience 57(7): 573-583.

Stachowicz, J.J., Byrnes, J.E. (2006) Species diversity, invasion success, and ecosystem functioning: disentangling the influence of resource competition, facilitation, and extrinsic factors. Marine Ecology Progress Series 311: 251-262.

Stachowicz, J.J., Fried, H., Osman, R.W., Whitlatch, R.B. (2002) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology 83(9): 2575-2590.

Stachowicz, J.J., Whitlatch, R.B., Osman, R.W. (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286: 1577-1579.

Stefaniak, L., Lambert, G., Gittenberger, A., Zhang, H., Lin, S., Whitlatch, R. (2009) Genetic conspecificity of the worldwide populations of *Didemnum vexillum* Kott, 2002. Aquatic Invasions 4(1): 29-44.

Stefaniak, L., Zhang, H., Gittenberger, A., Smtih, K., Holsinger, K., Lin, S., Whitlatch, R.B. (2012) Determining the native region of the putatively invasive ascidian *Didemnum vexillum* Kott, 2002. Journal of Experimental Marine Biology and Ecology 422-423: 64-71.

Streftaris, N., Zenetos, A., Papathanassiou, E. (2005) Globalisation in marine ecosystems: the story of non-indigenous marine species across European seas. Oceanography and Marine Biology: an Annual Review. 43: 419-453.

Sutherland, J.P. (1978) Functional roles of *Schizoporella* and *Styela* in the fouling community at Beaufort, North Carolina. Ecology 59: 257-264.

Svane, I., Young, C.M. (1989) The ecology and behaviour of ascidian larvae. Oceanography and Marine Biology: an Annual Review 27: 45-90.

Switzer, S.E., Therriault, T.W., Dunham, A., Pearce, C.M. (2012) Assessing potential control options for the invasive tunicate *Didiemnum vexillum* in shellfish aquaculture. Aquaculture 318: 145-153.

Thomson, R.E. (1981) Oceanography of the British Columbia coast. Canadian Special Publication of Fisheries and Aquatic Science 56: 1-291.

Tilman, D. (1997) Community invisibility, recruitment limitation, and grassland biodiversity. Ecology 78(1): 81-92.

Turner, S.J., Thrush, S.F., Cummings, V.J., Hewitt, J.E., Wilkinson, M.R., Williamson, R.B., Lee, D.J. (1997) Changes in epifaunal assemblages in response to marina operations and boating activities. Marine Environmental Research 43(3): 181-199.

Tyrell, M.C., Byers, J.E. (2007) Do artificial substrates favor nonindigenous fouling species over native species? Journal of Experimental Marine Biology and Ecology 342: 54-60.

Valentine, J.P., Johnson, C.R. (2003) Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages. Journal of Experimental Marine Biology and Ecology 295: 63-90.

Valentine, J.P., Johnson, C.R. (2005) Persistence of the exotic kelp *Undaria pinnatifida* does not depend on sea urchin grazing. Marine Ecology Progress Series 285: 43-55.

Valentine, P.C., Collie, J.S., Reid, R.N., Asch, R.G., Guida, V.G., Blackwood, D.S. (2007) The occurrence of the colonial ascidian *Didemnum* sp. on Georges Bank gravel habitat – Ecological observations and potential effects on groundfish and scallop fisheries. Journal of Experimental Marine Biology and Ecology 342: 179-181.

Vance, R.R., Schmitt, R.J. (1979) The effect of the predator-avoidance behavior of the sea urchin, *Centrostephanus coronatus*, on the breadth of its diet. Oecologia 44(1): 21-25.

Verling, E., Ruiz, G.M., Smith, L.D., Galil, B., Miller, A.W., Murphy, K.R. (2005) Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. Proceedings of the Royal Society B 272(1596): 1249-1257.

Vermeij, G.J. (1982) Phenotypic evolution in a poorly dispersing snail after arrival of a predator. Nature 299: 349-350.

Vitousek, P.M., D’Antonio, C.M., Loope, L.L., Westbrooks, R. (1996) Biological invasions as global environmental change. American Scientist 84: 468–478.

Wasson, K., Fenn, K., Pearse, J. (2005) Habitat differences in marine invasions of central California. Biological Invasions 7, 935-948.

White, L.F., Orr, L.C. (2011) Native clams facilitate invasive species in an eelgrass bed. Marine Ecology Progress Series 424: 87-95.

Whitlatch, R.B., Osman, R.W. (2009) Post-settlement predation on ascidian recruits: predator responses to changing prey density. Aquatic Invasions 4(1): 121-131.

Wilcove, D. S., Rothstein, D., Dubow, J., Phillips, A., Losos, E. (1998) Quantifying threats to imperiled species in the United States. BioScience 48(8): 607–615.

Wiliamson, M., Fitter, A. (1996) The varying success of invaders. Ecology 77(6): 1661-1666.

Williamson, M. (1996) Biological Invasions.Chapman & Hall, London.

Worcester, S.E. (1994) Adult rafting versus larval swimming: dispersal and recruitment of botryllid ascidian on eelgrass. Marine Biology 121: 309-317.

Young, C.M., Chia, F-S.(1984) Microhabitat-associated variability in survival and growth of subtidal solitary ascidians during the first 21 days after settlement. Marine Biology 81: 61-68.

Zaiko, A., Olenin, S., Daunys, D., Nalepa, T. (2007) Vulnerability of benthic habitats to the aquatic invasive species. Biological Invasions 9(6): 703-714.

Appendix A
Supporting Material for Chapter 2

Table A.1: List of 39 journals used to review the published literature from 1997-2010. Journal articles were searched via the ISI Web of Science search engine (Thomson Reuters Web of Science) and were used to identify field studies conducted on marine invertebrate and algal NIS.

General Ecology Journals:

American Naturalist
Ecology
Ecology Letters
Ecological Applications
Ecological Monographs
Conservation Biology
Oecologia
Oikos
Trends in Ecology and Evolution
Journal of Ecology
Journal of Animal Ecology
Journal of Biogeography
Diversity and Distributions
Austral Ecology
Biological Conservation

Multidisciplinary Science Journals:

Nature
Science
Proceedings of the National Academy of Sciences
Proceedings of the Royal Society, Biological Sciences

Marine Specific Journals:

Marine Ecology Progress Series
Canadian Journal of Fisheries and Aquatic Sciences
Aquatic Conservation-Marine and Freshwater Ecosystems
Marine Pollution Bulletin
Marine Biology
Journal of Experimental Marine Biology and Ecology
Estuarine Coastal and Shelf Science
Marine Environmental Research
Aquaculture
Aquatic Botany
Biological Bulletin
Estuaries and Coasts (just Estuaries before 06)
Biofouling
Limnology and Oceanography
Hydrobiologia
Journal of the Marine Biological Association, UK
Journal of Applied Phycology

Invasion Biology Journals:

Biological Invasions
Aquatic Invasions
Biological Control

Table A.2: Marine NIS reported within the 270 papers which conducted research in hard substrate habitats.

Phylum/Species	Taxon	Sessile/Mobile/Algae	Artificial	Natural	Source
Chlorophyta					
Caulerpa racemosa	Green Algae	Algae	X	X	**Artificial:** Vaselli et al. 2008 **Natural:** Piazzi et al. 2001; Piazzi & Ceccherelli 2002; Zuljevic et al. 2003; Klein et al. 2005; Piazzi et al. 2005; Ruitton et al. 2005; Piazzi & Ceccherelli 2006; Incera et al. 2010; Katsanevakis et al. 2010
Caulerpa taxifolia	Green Algae	Algae		X	BellanSantini et al. 1996; Meinesz et al. 2001; Ceccherelli et al. 2002; Piazzi & Ceccherelli 2002; Thibaut et al. 2004; Klein et al. 2005; Wright & Davis, 2006
Caulerpa webbiana	Green Algae	Algae	X	X	**Artificial:** Nieto Amat et al. 2008 **Natural:** Neito Amat et al. 2008
Codium fragile ssp. fragile	Green Algae	Algae	X	X	**Artificial:** Ashton et al. 2006; Bulleri et al. 2006a; Bulleri et al. 2006b; Neill et al. 2006; Vaselli et al. 2008 **Natural:** Trowbridge 1996; Harris & Tyrell 2001; Levin et al. 2002 Harris & Jones 2005; Sumi & Scheibling 2005; Neill et al. 2006; Scheibling & Gagnon 2006; D'Amours & Scheiblinng 2007; Dijkstra et al. 2007; Schmidt & Scheibling, 2007; Mineur et al. 2008; Pena & Barbara 2008; Watanabe et al. 2009
Ochrophyta					
Colpomenia peregrina	Brown Algae	Algae	X		Arenas et al. 2006; Minchin 2007; Mineur et al. 2008
Dictoyota dichotoma	Brown Algae	Algae	X	X	**Artificial:** Glasby et al. 2007; Dafforn et al. 2008 **Natural:** Glasby et al. 2007
Fucus evanescens	Brown Algae	Algae	X	X	**Artificial:** Wikstrom & Pavia 2004; **Natural:** Wikstrom & Kautsky 2004; Forslund et al. 2010
Sargassum muticum	Brown Algae	Algae	X	X	**Artificial:** Curiel et al. 1998; Cohen et al. 2005; Ashton et al. 2006; Minchin 2007; Kraan 2008 **Natural:** Viejo 1997; Andrew & Viejo 1998; Viejo 1999; Staehr et al. 2000; Arenas et al. 2002; Pedersen et al. 2005; Simkanin et al. 2005; Britton-Simmons 2006; Buschbaum et al. 2006; Klinger et al. 2006; Plouguerne et al. 2006; Sanchez & Fernandez 2006; Strong et al. 2006; Harries et al. 2007; White & Shurin 2007; Britton-Simmons & Abbott 2008; Kraan 2008; Mineur et al. 2008; Pena & Barbara 2008; Olabarria et al. 2009
Undaria pinnatifida	Brown Algae	Algae	X	X	**Artificial:** Curiel et al. 1998; Silva et al. 2002; Thornber et al. 2004; Cohen et al. 2005; Arenas et al. 2006; Russell et al. 2008; Zabin et al. 2009; Primo et al. 2010 **Natural:** Curiel et al. 1998; Forrest & Taylor 2002; Valentine & Johnson 2003; Casas et al. 2004; Edgar et al. 2004; Hewitt et al. 2005; Valentine & Johnson 2005 Pena & Barbara 2008; Peterio 2008; Russell et al. 2008; Raffo et al. 2009
Rhodophyta					
Acanthophora spicifera	Red Algae	Algae		X	Coles et al. 1999; Vermeij et al. 2010
Acrothamnion preissii	Red Algae	Algae		X	Klein et al. 2005
Anotrichium furcellatum	Red Algae	Algae	X		Arenas et al. 2006
Antithamnion amphigeneum	Red Algae	Algae		X	Klein et al. 2005
Antithamnion nipponicum	Red Algae	Algae		X	Rueness et al. 2007
Antithamnion pectinatum	Red Algae	Algae		X	Curiel et al. 1998
Antithamnionella boergesenii	Red Algae	Algae		X	Klein et al. 2005
Apoglossum gregarium	Red Algae	Algae		X	Klein et al. 2005
Asparagopsis armata	Red Algae	Algae		X	Klein et al. 2005; Kraan & Barrington 2005; Mineur et al. 2008
Asparagopsis taxiformis	Red Algae	Algae		X	Tsiamis & Panayotidis 2007
Bonnemaisonia hamifera	Red Algae	Algae		X	Harris & Tyrell 2001; Mineur et al. 2008
Caulacanthus ustulatus	Red Algae	Algae		X	Pister 2009
Chondria curvilineata	Red Algae	Algae		X	Klein et al. 2005
Dasya sessilis	Red Algae	Algae		X	Pena & Barbara, 2008
Falkenbergia rufolanosa	Red Algae	Algae		X	Klein et al. 2005
Goniotrichopsis sublittoralis	Red Algae	Algae		X	Klein et al. 2005

Table A.2 cont.

Phylum/Species	Taxon	Sessile/Mobile/Algae	Artificial	Natural	Source
Rhodophyta cont.					
Grateloupia doryphora	Red Algae	Algae	X	X	**Artificial:** Simon et al. 2001; **Natural:** Simon et al. 2001
Grateloupia luxurians	Red Algae	Algae	X		Arenas et al. 2006
Grateloupia turuturu	Red Algae	Algae	X		Arenas et al. 2006
Heterosiphonia japonica	Red Algae	Algae		X	Pena & Barbara, 2008
Hypnea musciformis	Red Algae	Algae		X	Vermeij et al. 2009
Hypnea spinella	Red Algae	Algae		X	Klein et al. 2005
Kappaphycus spp.	Red Algae	Algae		X	Conklin & Smith 2005
Laurencia caduciramulosa	Red Algae	Algae		X	Klein et al. 2005
Lomentaria hakodatensis	Red Algae	Algae	X		Cohen et al. 2005
Neosiphonia harveyi	Red Algae	Algae	X	X	**Artificial**: Arenas et al. 2006 **Natural:** Mineur et al. 2008; Pena & Barbara 2008
Polysiphonia atlantica	Red Algae	Algae		X	Klein et al. 2005
Polysiphonia harveyi	Red Algae	Algae		X	Klein et al. 2005
Womersleyella setacea	Red Algae	Algae		X	Klein et al. 2005; Antoniadou & Chintiroglou 2007
Porifera					
Chalinula nematifera	Sponge	Sessile	X		Avila & Carballo 2009
Cliona celata/lobata	Sponge	Sessile		X	Wasson et al. 2005
Gelloides fibrosa	Sponge	Sessile	X	X	**Artificial:** Coles et al. 1999 **Natural:** Demopoulos & Smith 2010
Halichondria bowerbanki	Sponge	Sessile	X	X	**Artificial:** Blum et al. 2007; **Natural:** Wasson et al. 2005
Haliciona loosanoffi	Sponge	Sessile	X		Wasson et al. 2001
Hymeniacidon sinapiumc	Sponge	Sessile	X	X	**Artificial:** Wasson et al. 2001; **Natural:** Wasson et al. 2005
Sigmadocia caerulea	Sponge	Sessile	X	X	**Artificial:** Coles et al. 1999 **Natural:** Demopoulos & Smith 2010
Suberites zeteki	Sponge	Sessile		X	Demopoulos & Smith 2010
Cnidaria					
Cordylophora caspia	Hydroid	Sessile	X	X	**Artificial:** Wasson et al. 2001; Zaiko et al. 2007 **Natural:** Zaiko et al. 2007
Diadumene franciscana	Anenome	Sessile	X		Wasson et al. 2001; Cohen et al. 2005
Diadumene leucolena	Anenome	Sessile	X		Wasson et al. 2001
Diadumene lineata	Anenome	Sessile	X		Cohen et al. 2005; Jewett et al. 2005
Diadumene sp.	Anenome	Sessile	X		Page et al. 2006
Eucheilota menoni	Hydroid	Sessile	X		Altuna 2009
Garveia franciscana	Hydroid	Sessile	X		Neves et al. 2007
Haliplanella lineata	Anenome	Sessile	X		Minchin 2007
Macrohynchia philippina	Hydroid	Sessile		X	Cinar 2006
Obelia dichotoma	Hydroid	Sessile	X		Wyatt et al. 2005
Oculina patagonica	Anenome	Sessile		X	Cinar 2006; Sartoretto et al. 2008
Tubastrae tagusensis	Coral	Sessile		X	Creed & Paula 2007

Table A.2

cont.

Phylum/Species	Taxon	Sessile/Mobile/Algae	Artificial	Natural	Source
Cnidaria cont.					
Tubastraea coccinea	Coral	Sessile		X	Creed & Paula 2007
Tubastraea micranthus	Coral	Sessile	X		Sammarco et al. 2010
Platyhelminthes					
Convoluta convoluta	Flatworm	Mobile		X	Rivest et al. 1999; Byrnes & Witman 2003
Entoprocta					
Barentisia benedeni	Kamptozoa	Sessile	X		Wasson et al. 2001
Ectoprocta					
Aetea anguina	Bryozoan	Sessile	X		Wyatt et al. 2005
Amathia distans	Bryozoan	Sessile	X		Floerl et al. 2009
Amathia vidovicic	Bryozoan	Sessile	X		Wasson et al. 2001
Anguinella palmata	Bryozoan	Sessile	X		Floerl et al. 2009
Barentisia benedeni	Kamptozoa	Sessile	X		Wasson et al. 2001
Bowerbankia gracilis	Bryozoan	Sessile	X		Wasson et al. 2005; Dafforn et al. 2009b
Bugula flabellata	Bryozoan	Sessile	X		Dafforn et al. 2008; Dafforn et al. 2000b; Floerl et al. 2009
Bugula neritina	Bryozoan	Sessile	X	X	**Artificial:** Wasson et al. 2001; Cohen et al. 2005; Wasson et al. 2005; Wyatt et al. 2005; Arenas et al. 2006; Altman & Whitlatch 2007; Blum et al. 2007; Dafforn et al. 2008; Dafforn et al. 2009a Dafforn et al. 2009b; Floerl et al. 2009; Sorte et al. 2010 **Natural:** Wasson et al. 2005; Pister 2009
Bugula stolonifera	Bryozoan	Sessile	X		Wasson et al. 2001; Wasson et al. 2005; Wyatt et al. 2005; Blum et al. 2007; Florel et al. 2009
Celleporaria nodulosa	Bryozoan	Sessile	X		Floerl et al. 2009
Conopeum seurati	Bryozoan	Sessile	X		Wyatt et al. 2005
Conopeum tenuissimum	Bryozoan	Sessile	X		Wasson et al. 2001; Wasson et al. 2005
Cryptosula pallasiana	Bryozoan	Sessile	X	X	**Artificial:** Wasson et al. 2001; Cohen et al. 2005; Wasson et al. 2005; Blum et al. 2007; Dafforn et al. 2009b; Floerl et al. 2009 **Natural:** Wasson et al. 2005
Cryptosula seurati	Bryozoan	Sessile	X		Dafforn et al. 2009b; Floerl et al. 2009
Cyclicopora longipora	Bryozoan	Sessile	X		Floerl et al. 2009
Electra angulata	Bryozoan	Sessile	X		Floerl et al. 2009
Membranipora membranacea	Bryozoan	Sessile	X	X	**Artificial:** Stachowicz et al. 2002a; Agius 2007; Altman & Whitlatch 2007; Tyrell & Byers 2007; Dijkstra & Harris 2009; Saunders & Metaxas 2009 **Natural:** Harris & Tyrell 2001; Levin et al. 2003; Saunders & Metaxas 2007; Saunders & Metaxas 2009
Microporella umbracula	Bryozoan	Sessile	X		Dafforn et al. 2009a
Rhynchozoon cf. larreyi	Bryozoan	Sessile	X		Floerl et al. 2009
Savignyella lafontii	Bryozoan	Sessile	X		Wyatt et al. 2005
Schizoporella errata	Bryozoan	Sessile	X		Wyatt et al. 2005; Glasby et al. 2007; Dafforn et al. 2008; Dafforn et al. 2009b; Floerl et al. 2009
Schizoporella pseudoerrata	Bryozoan	Sessile	X		Blum et al. 2007
Schizoporella unicornis	Bryozoan	Sessile	X	X	**Artificial:** Wasson et al. 2005; Sorte et al. 2010 **Natural:** Wasson et al. 2005
Scruparia ambigua	Bryozoan	Sessile	X		Floerl et al. 2009
Tricellaria catalinensis	Bryozoan	Sessile	X		Floerl et al. 2009

Table A.2 cont.

Phylum/Species	Taxon	Sessile/Mobile/Algae	Artificial	Natural	Source
Ectoprocta cont.					
Tricellaria inopinata	Bryozoan	Sessile	X		Occhipinti Ambrogi 2000; Arenas et al. 2006; Dafforn et al. 2008; Dafforn et al. 2009b
Watersipora arcuata	Bryozoan	Sessile	X		Cohen et al. 2005; Dafforn et al 2008; Floerl et al. 2009
Watersipora subtorquata	Bryozoan	Sessile	X	X	**Artificial:** Cohen et al. 2005; Wasson et al. 2005; Wyatt et al. 2005; Page et al. 2006; Blum et al. 2007; Glasby et al. 2007; Dafforn et al. 2008; Dafforn et al. 2009a; Dafforn et al. 2009b; Floerl et al. 2009; Grey 2009b; TerHorst & Dudgeon 2009; Sellheim et al. 2010; Sorte 2010 **Natural:** Glasby et al. 2007; Pister 2009
Zoobotryon verticellatum	Bryozoan	Sessile	X		Cohen et al. 2005; Wyatt et al. 2005; Amat & Tempera 2009; Floerl et al. 2009; Wirtz & Canning-Clode 2009
Mollusca					
Aplysia dactylomela	Gastropod	Mobile		X	Cinar et al. 2006; Pasternak & Galil, 2010
Batillaria attramentaria	Gastropod	Mobile		X	Wasson et al. 2005
Brachidontes pharaonis	Bivalve	Sessile		X	Rilov et al. 2002; Dogan et al. 2007
Bursatella leachii	Nudibranch	Mobile		X	Daskos & Zenetos 2007
Charma elatensis	Bivalve	Sessile	X		Coles et al. 1999
Chromodoris annulata	Nudibranch	Mobile		X	Daskos & Zenetos 2007; Gökoğlu & Özgür, 2008
Crassostrea gigas	Bivalve	Sessile	X	X	**Artificial:** Cohen et al. 2005; Cognie et al. 2006; Grey 2009b **Natural:** Cognie et al. 2006; Diederich 2006; Klinger et al. 2006; Ruesink 2007
Crepidula aculeata	Gastropod	Mobile		X	Coles et al. 1999
Crepidula fornicata	Gastropod	Mobile	X	X	**Artificial:** Arenas et al. 2006; **Natural:** Thieltges et al. 2004; Thieltges 2005
Crepipatella dilata	Patellid	Mobile	X		Collin et al. 2009
Geukensia demissa	Bivalve	Sessile	X		Cohen et al. 2005
Isognomon bicolor	Bivalve	Sessile		X	Breves-Ramos et al. 2010
Littorina littorea	Gastropod	Mobile		X	Eastwood et al. 2007
Musculista senhousia	Bivalve	Sessile	X		Cohen et al. 2005
Mytilopsis leucophaeata	Bivalve	Sessile		X	Laine et al. 2006
Mytilopsis trautwineana	Bivalve	Sessile	X		Aldridge et al. 2008
Mytilus galloprovincialis	Bivalve	Sessile	X	X	**Artificial:** Cohen et al. 2005; Braby & Somero 2006; Johnson & Geller 2006; Pister 2009; Sellheim et al. 2010 **Natural:** McQuaid & Philips 2000; Sebastian et al. 2002; Steffani & Branch 2003; Steffani & Branch 2005;Wasson et al. 2005;Bownes & McQuaid 2006; Erlandsson et al. 2006; Ruis & McQuaid 2006; Zardi et al. 2006; Porri et al. 2007; Robinson et al. 2007; Schneider & Helmuth 2007; Zardi et al. 2007; Branch et al. 2008; Hanekom 2008; von der Meden et al. 2008; Zardi et al. 2008; Pister 2009; von der Meden et al. 2010
Ocinebrellus inornatus	Gastropod	Mobile	X	X	**Artificial:** Faasse & Ligthart 2009 **Natural:** Martel et al. 2004; Faasse & Ligthart 2009
Okenia plana	Gastropod	Mobile	X		Wasson et al. 2001
Perna perna	Bivalve	Sessile	X		Hicks et al. 2001
Philine auriformis	Gastropod	Mobile	X		Wasson et al. 2001
Potamopygus antipodarum	Gastropod	Mobile		X	Zaiko et al. 2007; Bersine et al. 2008; Brenneis et al. 2010
Rapana venosa	Gastropod	Mobile		X	Mann & Harding 2000; Mann et al. 2006
Septifer bilocularis	Patellid	Mobile		X	Albayrak & Caglar 2006
Siphonaria belcheri	Patellid	Mobile		X	Albayrak & Caglar 2006
Teredo bartschi	Bivalve	Sessile	X		Cohen et al. 2005
Urosalpinx cinerea	Gastropod	Mobile	X	X	**Artificial:** Faasse & Ligthart, 2009 **Natural:** Faasse & Ligthart, 2009

Table A.2 cont.

Phylum/Species	Taxon	Sessile/Mobile/Algae	Artificial	Natural	Source
Annelida					
Amblyosyllis speciosa	Polychaete	Mobile	X		Cohen et al. 2005
Boccardia knoxi	Polychaete	Mobile		X	Sato-Okoshi et al. 2008
Branchiomma luctuosum	Polychaete	Sessile		X	Cinar et al. 2006
Branchiosyllis exilis	Polychaete	Mobile	X		Cohen et al. 2005
Dipolydora aciculata	Polychaete	Mobile		X	Sato-Okoshi et al. 2008
Ficopomatus enigmaticus	Polychaete	Sessile	X	X	**Artificial:** Cohen et al. 2005; Jewett et al. 2005; Wasson et al. 2005; Arenas et al. 2006; Blum et al. 2007; Minchin 2007; **Natural:** Schwindt et al. 2001
Hydroides brachyacanthus	Polychaete	Sessile		X	Cinar 2006
Hydroides diramphus	Polychaete	Sessile	X	X	**Artificial:** Cohen et al. 2005; Dafforn et al. 2009b **Natural:** Cinar 2006
Hydroides elegans	Polychaete	Sessile	X	X	**Artificial:** Cohen et al. 2005; Blum et al. 2007; Glasby et al. 2007; Dafforn et al. 2008; Dafforn et al. 2009a; Dafforn et al. 2009b **Natural:** Cinar 2006; Glasby et al. 2007
Hydroides ezoensis	Polychaete	Sessile	X		Arenas et al. 2006
Hydroides heterocerus	Polychaete	Sessile		X	Cinar 2006
Hydroides homoceros	Polychaete	Sessile		X	Cinar 2006
Hydroides minax	Polychaete	Sessile		X	Cinar 2006
Hydroides operculatus	Polychaete	Sessile		X	Cinar 2006
Hydroides sanctaecrucis	Polychaete	Sessile	X		Lewis et al. 2006
Marenzelleria viridis	Polychaete	Mobile		X	Zaiko et al. 2007
Myrianida pachycera	Polychaete	Mobile	X		Cohen et al. 2005
Polydora aura	Polychaete	Mobile		X	Sato-Okoshi et al. 2008
Polydora cornuta	Polychaete	Mobile	X		Neves et al. 2007
Polydora uncinata	Polychaete	Mobile		X	Sato-Okoshi et al. 2008
Spirobranchus (s yn. *Pomatoleios) kraussii*	Polychaete	Sessile		X	Cinar 2006
Pseudonereis anomala	Polychaete	Mobile	X		Kambouroglou & Nicolaidou, 2006
Pseudopolydora paucibranchiata	Polychaete	Mobile	X	X	**Artificial:** Cohen et al. 2005; **Natural:** Wasson et al. 2005
Sabella spallanzanii	Polychaete	Sessile	X		Currie et al. 2000; Holloway & Keough 2002a; Holloway & Keough 2002b
Spirobranchus tetraceros	Polychaete	Sessile		X	Cinar 2006
Streblospio benedicti	Polychaete	Mobile		X	Wasson et al. 2005
Terebrasabella heterouncinata	Polychaete	Sessile		X	Culver & Kurisk 2000
Typosyllis nipponica	Polychaete	Mobile	X		Cohen et al. 2005
Arthropoda					
Ammothella hilgendorfi	Pycnogonid	Mobile	X		Cohen et al. 2005
Amphibalanus amphitrite	Barnacle	Sessile	X		Dafforn et al. 2009b

Table A.2 cont.

Phylum/Species	Taxon	Sessile/Mobile/Algae	Artificial	Natural	Source
Arthropoda cont.					
Amphibalanus reticulatus	Barnacle	Sessile	X		Neves et al. 2007
Ampithoe valida	Amphipod	Mobile	X		Cohen et al. 2005
Aoriodes secundus	Amphipod	Mobile	X		Cohen et al. 2005
Atergatis roseus	Crab	Mobile		X	Yokes et al. 2007
Austrominius (syn *Elminius) modestus*	Barnacle	Sessile	X	X	**Artificial:** Arenas et al. 2006; Minchin 2007; **Natural:** Lawson et al. 2004; Simkanin et al. 2005; Watson et al. 2005; Witte et al. 2010
Balanus amphitrite	Barnacle	Sessile	X	X	**Artificial:** Cohen et al. 2005 **Natural:** Demopoulos et al. 2010
Balanus eburneus	Barnacle	Sessile	X		Cohen et al. 2005
Balanus glandula	Barnacle	Sessile	X	X	**Artificial:** Kado 2003; Savoya & Schwindt 2010 **Natural:** Schwindt 2007
Balanus improvisus	Barnacle	Sessile	X	X	**Artificial:** Wasson et al. 2001; Wasson et al. 2005; Blum et al. 2007; Minchin 2007 **Natural:** Zaiko et al. 2007
Balanus reticulatus	Barnacle	Sessile		X	Demopoulos & Smith 2010
Callinectes sapidus	Crab	Mobile	X		Cabal et al. 2006
Caprella mutica	Amphipod	Mobile	X	X	**Artificial:** Willis et al. 2004; Cohen et al. 2005; Arenas et al. 2006; Ashton et al. 2006; Page et al. 2006; Ashton et al. 2007; Minchon 2007; Page et al. 2007; Frey et al. 2009 **Natural:** Page et al. 2006; Page et al. 2007
Caprella scaura	Amphipod	Mobile	X		Martinez & Adarraga 2008
Caprella simia	Amphipod	Mobile	X		Cohen et al. 2005
Carcinus maenas	Crab	Mobile		X	Torchin et al. 2001; Jensen et al. 2002; Lohrer & Whitlatch 2002a; Lohrer & Whitlatch 2002b; Smith 2004; Ahyong, 2005; Cameron & Metaxas 2005; Hidalgo et al. 2005; Eastwood et al. 2007; Delaney et al. 2008; Delaney & Leung 2010
Carupa tenuipes	Crab	Mobile		X	Yokes et al. 2007; Pancucci-Papadopoulou et al. 2009
Chaetogammarus ischnus	Amphipod	Mobile		X	Zaiko et al. 2007
Chaetogammarus warpachowskyi	Amphipod	Mobile		X	Zaiko et al. 2007
Charybdis hellerii	Crab	Mobile		X	Yokes et al. 2007
Charybdis japonica	Crab	Mobile	X	X	**Artificial:** Gust & Inglis 2006; **Natural:** Gust & Inglis 2006
Charybdis longicollis	Crab	Mobile		X	Yokes et al. 2007
Chelicorophium curvispinum	Amphipod	Mobile		X	Zaiko et al. 2007
Chelura terebrans	Amphipod	Mobile	X		Cohen et al. 2005
Chthamalus proteus	Barnacle	Sessile	X	X	**Artificial:** Zabin & Altieri 2007; Zabin et al. 2007; **Natural:** Coles et al. 1999; Zabin et al. 2007; Demopoulos & Smith 2010
Elasmopus rapax	Amphipod	Mobile	X		Cohen et al. 2005
Ericthonius brasiliensis	Amphipod	Mobile	X		Cohen et al. 2005; Page et al. 2007
Gammaropsis togoensis	Amphipod	Mobile	X	X	**Artificial:** Bakir et al 2007; **Natural:** Bakir et al 2007
Gammarus tigrinus	Amphipod	Mobile		X	Zaiko et al. 2007
Grandidierella japonica	Amphipod	Mobile	X	X	**Artificial:** Wasson et al. 2001; Cohen et al. 2005; Wasson et al. 2005; **Natural:** Wasson et al. 2005
Hamimysis anomala	Mysid	Mobile		X	Zaiko et al. 2007
Hemigrapsus sanguineus	Crab	Mobile		X	Gerard et al. 1999; Lohrer et al. 2000a; Lohrer et al. 2000b; Lohrer & Whitlatch 2002a; Lohrer & Whitlatch 2002b; Jensen et al. 2003; Brousseau & Goldberg 2007; Delaney et al. 2008; Dauvin 2009a; Dauvin 2009b; Dauvin et al. 2009; Stephenson et al. 2009; Altieri et al. 2010; Delaney & Leung 2010
Hemigrapsus takanoi	Crab	Mobile		X	Dauvin et al. 2009

Table A.2 cont.

Phylum/Species	Taxon	Sessile/Mobile/Algae	Artificial	Natural	Source
Arthropoda cont.					
Iais californica	Isopod	Mobile	X		Wasson et al. 2001
Ianiropsis tridens	Isopod	Mobile	X		Cohen et al. 2005
Jassa marmorata	Amphipod	Mobile	X		Cohen et al. 2005
Leucothoe alata	Amphipod	Mobile	X		Cohen et al. 2005
Ligia exotica	Isopod	Mobile		X	Tsai & Dai 2001
Limnomysis benedeni	Mysid	Mobile		X	Zaiko et al. 2007
Limnoria tripunctata	Isopod	Mobile	X		Cohen et al. 2005
Megabalanus coccopoma	Barnacle	Sessile	X	X	**Artificial:** Dafforn et al. 2009b; Yamaguchi et al. 2009 **Natural:** Yamaguchi et al. 2009
Melicertus hathor	Shrimp	Mobile		X	Yokes et al. 2007
Melita palmata	Amphipod	Mobile		X	Obenat et al. 2006
Micippa thalia	Crab	Mobile		X	Yokes et al. 2007
Monocorophium acherusicum	Amphipod	Mobile	X	X	**Artificial:** Cohen et al. 2005; Wasson et al. 2005; **Natural:** Wasson et al. 2005
Monocorophium insidiosum	Amphipod	Mobile	X		Cohen et al. 2005; Minchin 2007
Monocorophium sextonae	Amphipod	Mobile	X		Michin 2007
Nanosesarma minutum	Crab	Mobile		X	Coles et al. 1999
Obessogammarus crassus	Amphipod	Mobile	X	X	**Artificial:** Zaiko et al. 2007; **Natural:** Zaiko et al. 2007
Palaemon longirostris	Shrimp	Mobile		X	Sezgin et al. 2007
Palaemon macrodactylus	Shrimp	Mobile	X	X	**Artificial:** Cohen et al. 2005 **Natural:** Chicharo et al. 2009
Panopeus lacustris	Crab	Mobile		X	Demopoulos & Smith 2010
Paradexamine cf. churinga	Amphipod	Mobile	X		Cohen et al. 2005
Paralithodes camtschaticus	Crab	Mobile		X	Faccia et al. 2009
Paramysis lacustris	Mysid	Mobile		X	Zaiko et al. 2007
Paranthura japonica	Isopod	Mobile	X		Cohen et al. 2005
Percnon gibbesi	Crab	Mobile		X	Deurdero et al. 2005; Yokes & Galil 2006; Elkrwe et al. 2008
Petrolisthes armatus	Crab	Mobile		X	Hollebone & Hay 2007; Hollebone & Hay 2008
Pontogammarus robustoides	Amphipod	Mobile	X	X	**Artificial:** Zaiko et al. 2007; **Natural:** Zaiko et al. 2007
Portunus pelagicus	Crab	Mobile		X	Yokes et al. 2007
Pyromaia tuberculata	Crab	Mobile		X	Ahyong 2006
Rhithropanopeus harrisii	Crab	Mobile		X	Roche & Torchin 2007; Roche et al. 2009
Scylla serrata	Crab	Mobile		X	Demopoulos & Smith 2010
Sinelobus cf. stanfordi	Isopod	Mobile	X		Cohen et al. 2005
Sphaeroma quoyanum	Isopod	Mobile	X	X	**Artificial:** Wasson et al. 2001; Cohen et al. 2005; Davidson et al. 2008a; Davidson et al. 2008b **Natural:** Davidson et al. 2008a; Davidson et al. 2008b

Table A.2 cont.

Phylum/Species	Taxon	Sessile/Mobile/Algae	Artificial	Natural	Source
Arthropoda cont.					
Stenothoe valida	Amphipod	Mobile	X		Cohen et al. 2005
Striatobalnus amaryllis	Barnacle	Sessile	X		Neves et al. 2007
Thalamita poissonii	Crab	Mobile		X	Yokes et al. 2007
Echinodermata					
Diadema setosum	Sea Urchin	Mobile		X	Yokes & Galil 2006
Synaptula reciprocans	Holothurian	Mobile	X	X	**Artificial:** Antoniadou & Vafidis 2009 **Natural:** Cinar et al. 2006
Chordata/Ascidiacea					
Ascidia sydneiensis	Ascidian	Sessile	X		Rocha et al. 2009
Ascidia zara	Ascidian	Sessile	X		Lambert & Lambert 1998; Lambert & Lambert 2003; Cohen et al. 2005; Blum et al. 2007
Ascidiella aspersa	Ascidian	Sessile	X		**Artificial:** Stachowicz et al. 2002a; Stachowicz et al. 2002b; Aguis 2007; Alman & Whitlatch 2007; Rajbanshi & Pederson 2007; Dijkstra & Harris 2009; Carman et al. 2009 Carman & Grunden 2010
Bostrichobranchus pilularis	Ascidian	Sessile	X		Lambert & Lambert 1998
Botrylloides leachi	Ascidian	Sessile	X		Dafforn et al. 2008; Dafforn et al. 2009a; Dafforn et al. 2009b
Botrylloides perspicuum	Ascidian	Sessile	X		Lambert & Lambert 2003; Cohen et al. 2005
Botrylloides violaceus	Ascidian	Sessile	X	X	**Artificial:** Stachowicz et al. 1999; Wasson et al. 2001; Stachowicz et al. 2002a; Stachowicz et al. 2002b; Lambert & Lambert 2003; Cohen et al. 2005; Arenas et al. 2006; Altman & Whtilatch 2007; Agius 2007; Arenas et al. 2007; Blum et al. 2007; Dijkstra et al. 2007a; Dijkstra et al. 2007b; Minchin 2007; Rajbanshi & Pederson 2007; Tyrrell & Byers 2007; Dafforn et al. 2008; Dijkstra & Harris 2009; Grey 2009a; Grey 2009b; Grey 2010; Sorte et al. 2010; Callahan et al. 2010; Carman et al. 2009; Carman & Grunden 2010 **Natural:** Grosholz 2001; Harris & Tyrell; 2001; Wasson et al. 2005; Dijkstra et al. 2007a; Simoncini & Miller 2007; Carman et al. 2009; Carman & Grunden 2010; Callahan et al. 2010
Botryllus schlosseri	Ascidian	Sessile	X	X	**Artificial:** Lambert & Lambert 1998; Lambert & Lambert 2003; Cohen et al. 2005; Jewett et al. 2005; Agius 2007; Altman & Whtilatch 2007; Blum et al 2007; Dijkstra et al. 2007a; Tyrrell & Byers 2007; Dafforn et al. 2008; Carman et al. 2009; Dafforn et al. 2009; Grey 2009a; Grey 2009b; Callahan et al. 2010; Carman & Grunden 2010 **Natural:** Dijkstra et al. 2007a
Ciona intestinalis	Ascidian	Sessile	X		Lambert & Lambert 1998; Lambert & Lambert 2003; McDonald 2004; Cohen et al. 2005; Blum et al. 2007; Rajbanshi & Pederson, 2007; Lutz-Collins et al. 2009; Ramsay et al. 2009
Ciona savignyi	Ascidian	Sessile	X		Lambert & Lambert 1998; Lambert & Lambert 2003; Cohen et al. 2005; Blum et al. 2007; Smith et al. 2010
Clavelina cyclus	Ascidian	Sessile	X	X	Chavanich et al. 2009
Clavelina lepadiformis	Ascidian	Sessile	X	X	Reinhardt et al. 2010
Corella eumyota	Ascidian	Sessile	X	X	**Artificial**: Lambert 2004; Arenas et al. 2006; Minchin 2007; Collin et al. 2010; Nagar et al. 2010 **Natural**: Collin et al. 2010
Didemnum perlucidum	Ascidian	Sessile	X		Kremer et al. 2010
Didemnum vexillum	Ascidian	Sessile	X	X	**Artificial:** Dunstan & Johnson 2004; Minchin & Sides 2006; Agius 2007; Altman & Whitlatch 2007; Blum et al. 2007; Bullard et al. 2007; Carman 2007; Couts & Forrest 2007; Dijkstra et al. 2007a; Dijkstra et al. 2007b; Minchin 2007; Osman & Whitlatch 2007; Carman et al. 2009; Dijkstra & Harris, 2009; Griffith et al. 2009; Valentine et al. 2009; Carman & Grunden 2010 **Natural:** Bullard et al. 2007; Carman 2007; Dijkstra et al. 2007a; Gittenberger 2007; Osman & Whitlatch 2007; Carman et al. 2009; Lengyel et al. 2009; Mercer et al. 2009; Valentine et al. 2009
Diplosoma listerianum	Ascidian	Sessile	X	X	**Artificial:** Stachowicz et al. 2002a; Stachowicz et al. 2002b; Agius 2007; Altman & Whitlatch 2007; Blum et al. 2007; Dijkstra et al. 2007a; Dijkstra et al. 2007b; Dafforn et al. 2008; Dafforn et al. 2009a; Dafforn et al. 2009b; Dijkstra & Harris, 2009; Grey 2009a; Grey 2009b; Carman & Grunden 2010; Sorte et al. 2010 **Natural:** Harris & Tyrell 2001; Dijkstra et al. 2007a
Ecteinascidia thurstoni	Ascidian	Sessile	X		Chavanich et al. 2009
Herdmania momus	Ascidian	Sessile	X	X	**Artificial**: Shenkar & Loya 2008 **Natural**: Cinar et al. 2006
Microcosmus squamiger	Ascidian	Sessile	X		Lambert & Lambert 1998; Lambert & Lambert 2003; Cohen et al. 2005; Ruis et al. 2009

Table A.2 cont.

Phylum/Species	Taxon	Sessile/Mobile/Algae	Artificial	Natural	Source
Chordata/Ascidiacea cont.					
Mogula citrina	Ascidian	Sessile	X		Lambert et al. 2010
Molgula manhattensis	Ascidian	Sessile	X	X	**Artificial:** Lambert & Lambert 1998; Wasson et al. 2001; Lambert & Lambert 2003; Cohen et al. 2005; Blum et al. 2007; **Natural:** Wasson et al. 2005
Perophora japonica	Ascidian	Sessile	X	X	**Artificial:** Lambert 2005; Arenas et al. 2006; **Natural:** Baldock & Bishop 2001;
Phallusia nigra	Ascidian	Sessile	X	X	**Artificial:** Cinar et al. 2006; Kondilatos et al. 2010 **Natural:** Cinar et al. 2006; Kondilatos et al. 2010
Polyandrocarpa zorritensis	Ascidian	Sessile	X		Lambert & Lambert 1998; Lambert & Lambert 2003; Cohen et al. 2005
Pyura praeputalis	Ascidian	Sessile		X	Castilla et al. 2004a; Castillia et al. 2004b
Styela canopus	Ascidian	Sessile	X		Lambert & Lambert 1998; Lambert & Lambert 2003; Cohen et al. 2005
Styela clava	Ascidian	Sessile	X		**Artificial:** Lambert & Lambert 1998; Lambert & Lambert 1998; Stachowicz et al. 2002a; Cohen et al. 2005; Arenas et al. 2006; Ashton et al. 2006; Minchin et al. 2006; Agius 2007; Altman & Whitlatch 2007; Blum et al. 2007; Bourque et al. 2007; Davis et al. 2007; Krone et al. 2007; Minchin 2007; Arsenault et al. 2009; Carman et al. 2009; Davis & Davis 2009; Dijkstra & Harris, 2009; Grey 2009a Grey 2009b; Nunn & Minchin, 2009; Carman & Grunden 2010 **Natural:** Davis & Davis 2008; Nunn & Minchin 2009
Styela plicata	Ascidian	Sessile	X	X	**Artificial:** Lambert & Lambert 1998; Lambert & Lambert, 2003; Cohen et al. 2005; Wyatt et al. 2005; Glasby et al. 2007; Dafforn et al. 2008; Dafforn et al. 2009a; Dafforn et al. 2009b **Natural:** Glasby et al. 2007
Symplegma brakenhielmi (=S. oceania)	Ascidian	Sessile	X		Lambert & Lambert 1998; Cinar et al. 2006
Symplegma reptans	Ascidian	Sessile	X		Lambert & Lambert 1998; Coles et al. 1999; Lambert & Lambert 2003; Cohen et al. 2005

Bibliography for Table A.2: Bibliography of literature assessed throughout the review. Journal articles from 1997-2010 were searched via the ISI Web of Science search engine (Thomson Reuters Web of Science) and were used to identify field studies conducted on marine invertebrate and algal NIS.

Agius, BP (2007) Spatial and temporal effects of pre-seeding plates with invasive ascidians: Growth, recruitment and community composition. Journal of Experimental Marine Biology and Ecology 342: 30-39

Ahyong, ST (2005) Range extension of two invasive crab species in eastern Australia: *Carcinus maenas* (Linnaeus) and *Pyromaia tuberculata* (Lockington). Marine Pollution Bulletin 50: 460-462

Albayrak, S; Caglar, S (2006) On the presence of *Siphonaria belcheri* Hanley, 1858 {Gastropoda: Siphonariidae} and *Septifer bilocularis* (Linnaeus, 1758) {Bivalvia: Mytilidae} in the Iskenderun Bay (SE Turkey). Aquatic Invasions 1(4): 292-294

Altman, S; Whitlatch, RB (2007) Effects of small-scale disturbance on invasion success in marine communities. Journal of Experimental Marine Biology and Ecology 342: 15-29

Andrew, N.L. & Viejo, R.M. (1998) Ecologicla limits to the invasion of *Sargassum muticum* in northern Spain. Aquatic Botany 60: 251-263

Antoniadou, C; Chintiroglou, C (2007) Zoobenthos associated with the invasive red alga *Womersleyella setacea* (Rhodomelacea) in the northern Aegean Sea. Journal of the Marine Biological Association of the United Kingdom 87: 629-641

Arenas, F; Bishop, JDD; Carlton, JT; Dyrynda, PJ; Farnham, WF; Gonzalez, DJ; Jacobs, MW; Lambert, C; Lambert, G; Nielsen, SE; Pederson, JA; Porter, JS; Ward, S; Wood, CA (2006) Allen species and other notable records from a rapid assessment survey of marinas on the south coast of England. Journal of the Marine Biological Association of the United Kingdom 86: 1329-1338

Arenas, F; Viejo, RM; Fernandez, C (2002) Density-dependent regulation in an invasive seaweed: responses at plant and modular levels. Journal of Ecology 90: 820-829

Ashton, GV; Boos, K; Shucksmith, R; Cook, E (2006) Rapid assessment of the distribution of marine non-native species in marinas in Scotland. Aquatic Invasions 1(4): 209-213

Ashton, GV; Willis, KJ; Cook, EJ; Burrows, M (2007) Distribution of the introduced amphipod, *Caprella mutica* Schurin, 1935 (Amphipoda : Caprellida : Caprellidae) on the west coast of Scotland and a review of its global distribution. Hydrobiologia 590: 31-41

Bakir, K; Sezgin, M; Katagan, T (2007) Contribution to the knowledge of alien amphipods off the Turkish coast: *Gammaropsis togoensis* (Schellenberg, 1925). Aquatic Invasions 2(1): 80-82

Baldock, B; Bishop, JDD (2001) Occurrence of the non-native ascidian *Perophora japonica* in the Fleet, southern England. Journal of the Marine Biological Association of the United Kingdom 81: 1067-1067

Blum, JC; Chang, AL; Liljesthrom, M; Schenk, ME; Steinberg, MK; Ruiz, GM (2007) The non-native solitary ascidian *Ciona intestinalis* (L.) depresses species richness. Journal of Experimental Marine Biology and Ecology 342: 5-14

Bourque, D; Davidson, J; MacNair, NG; Arsenault, G; LeBlanc, AR; Landry, T; Miron, G (2007) Reproduction and early life history of an invasive ascidian *Styela clava* Herdman in Prince Edward Island, Canada. Journal of Experimental Marine Biology and Ecology 342: 78-84

Bownes, SJ; McQuaid, CD (2006) Will the invasive mussel *Mytilus galloprovincialis* Lamarck replace the indigenous *Perna perna* L. on the south coast of South Africa?. Journal of Experimental Marine Biology and Ecology 338: 140-151

Braby, CE; Somero, GN (2006) Ecological gradients and relative abundance of native (*Mytilus trossulus*) and invasive (*Mytilus galloprovincialis*) blue mussels in the California hybrid zone. Marine Biology 148: 1249-1262

Britton-Simmons, KH (2006) Functional group diversity, resource preemption and the genesis of invasion resistance in a community of marine algae. Oikos 113: 395-401

Brousseau, DJ; Goldberg, R (2007) Effect of predation by the invasive crab Hemigrapsus sanguineus on recruiting barnacles Semibalanus balanoides in western Long Island Sound, USA. Marine Ecology-Progress Series 339: 221-228

Bullard, SG; Lambert, G; Carman, MR; Byrnes, J; Whitlatch, RB; Ruiz, G; Miller, RJ; Harris, L; Valentine, PC; Collie, JS; Pederson, J; McNaught, DC; Cohen, AN; Asch, RG; Dijkstra, J; Heinonen, K (2007) The colonial ascidian *Didemnum* sp A: Current distribution, basic biology and potential threat to marine communities of the northeast and west coasts of North America. Journal of Experimental Marine Biology and Ecology 342: 99-108

Bulleri, F; Abbiati, M; Airoldi, L (2006a) The colonisation of human-made structures by the invasive alga *Codium fragile* ssp *tomentosoides* in the north Adriatic Sea (NE Mediterranean). Hydrobiologia 555: 263-269

Bulleri, F; Airoldi, L; Branca, GM; Abbiati, M (2006b) Positive effects of the introduced green alga, *Codium fragile* ssp *tomentosoides*, on recruitment and survival of mussels. Marine Biology 148: 1213-1220

Buschbaum, C; Chapman, AS; Saier, B (2006) How an introduced seaweed can affect epibiota diversity in different coastal systems. Marine Biology 148: 743-754

Byers, JE (2000) Differential susceptibility to hypoxia aids estuarine invasion. . Marine Ecology-Progress Series 203: 123-132

Byrnes, J; Witman, JD (2003) Impact assessment of an invasive flatworm, *Convoluta convoluta*, in the Southern Gulf of Maine. Journal of Experimental Marine Biology and Ecology 293: 173-191

Cabal, J; Millan, JAP; Arronte, JC (2006) A new record *of Callinectes sapidus* Rathbun, 1896 (Crustacea: Decapoda: Brachyura) from the Cantabrian Sea, Bay of Biscay, Spain. Aquatic Invasions 1(3): 186-187

Cameron, B; Metaxas, A (2005) Invasive green crab, *Carcinus maenas*, on the Atlantic coast and in the Bras d'Or Lakes of Nova Scotia, Canada: larval supply and recruitment. Journal of the Marine Biological Association of the United Kingdom 85: 847-855

Carman, MR (2007) Benthic foraminifera associated with the invasive ascidian, *Didemnum* sp A. Journal of Experimental Marine Biology and Ecology 342: 147-153

Casas, G., Scrosati, R. & Luz Piriz M. (2004) The invasive kelp *Undaria pinnatifida* (Phaeophyceae, Laminariales) reduces native seaweed diversity in Nuevo Gulf (Patagonia, Argentina). Biological Invasions 6: 411-416

Castilla, JC; Guinez, R; Caro, AU; Ortiz, V (2004b) Invasion of a rocky intertidal shore by the tunicate *Pyura praeputialis* in the Bay of Antofagasta, Chile. Proceedings of the National Academy of Sciences of the United States of America 101: 8517-8524

Castilla, JC; Lagos, NA; Cerda, M (2004a) Marine ecosystem engineering by the alien ascidian *Pyura praeputialis* on a mid-intertidal rocky shore. Marine Ecology-Progress Series 268: 119-130

Ceccherelli, G; Piazzi, L; Balata, D (2002) Spread of introduced *Caulerpa* species in macroalgal habitats. Journal of Experimental Marine Biology and Ecology 280: 1-11

Cinar, ME (2006) Serpulid species (Polychaeta: Serpulidae) from the Levantine coast of Turkey (eastern Mediterranean) with special emphasis on alien species. Aquatic Invasions 1(4): 223-240

Cinar, ME; Bilecenoglu, M; Ozturk, B; Can, A (2006) New records of alien species on the Levantine coast of Turkey. Aquatic Invasions 1(2); 84-90

Clark, GF; Johnston, EL (2005) Manipulating larval supply in the field: a controlled study of marine invasibility. Marine Ecology-Progress Series 298: 9-19

Cognie, B., Haure, J. & Barille, L. (2006) Spatial distribution in a temperate coastal ecosystem of the wild stock of the farmed oyster *Crassostrea gigas* (Thunberg). Aquculture 259:249-259

Cohen, A.N., Harris, L.H., Bingham, B.L., Carlton, J.T., Chapman, J.W., Lambert, C.C., Lambert, G., Ljubenkov, J.C., Murray, S.N., Rao, L.C., Reardon, K. & Schwindt, E. (2005) Rapid assessment survey for exotic organisms in southern California bays and harbors, and abundance in port and non-port areas. Biological Invasions 7: 995-1002

Coles, SL; DeFelice, RC; Eldredge, LG; Carlton, JT (1999) Historical and recent introductions of non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian Islands. Marine Biology 135: 147-158

Conklin, E.J. and Smith, J.E. (2005) Abundance and spread of the invasive red algae, *Kappaphycus* spp., in Kane'ohe Bay, Hawaii and an experimental assessment of management options. Biological Invasions 7: 1029-1039

Coutts, ADM; Forrest, BM (2007) Development and application of tools for incursion response: Lessons learned from the management of the fouling pest *Didemnum vexillum*. Journal of Experimental Marine Biology and Ecology 342: 154-162

Creed, JC; De Paula, AF (2007) Substratum preference during recruitment of two invasive alien corals onto shallow-subtidal tropical rocky shores. Marine Ecology-Progress Series 330: 101-111

Culver, CS; Kurisk, AM (2000) The apparent eradication of a locally established introduced marine pest. Biological Invasions 2: 245-253

Curiel, D; Bellemo, G; Marzocchi, M; Scattolin, M; Parisi, G (1998) Distribution of introduced Japanese macroalgae *Undaria pinnatifida*, *Sargassum muticum* (Phaeophyta) and *Antithamnion pectinatum* (Rhodophyta) in the Lagoon of Venice. Hydrobiologia 385: 17-22

Currie, DR; McArthur, MA; Cohen, BF (2000) Reproduction and distribution of the invasive European fanworm *Sabella spallanzanii* (Polychaeta : Sabellidae) in Port Phillip Bay, Victoria, Australia. Marine Biology 136: 645-656

D'Amours, O; Scheibling, RE (2007) Effect of wave exposure on morphology, attachment strength and survival of the invasive green alga *Codium fragile* ssp *tomentosoides*. Journal of Experimental Marine Biology and Ecology 351: 129-142

Daskos, A; Zenetos, A (2007) Additions to the knowledge of alien Opisthobranchia of Greece. Aquatic Invasions 2(3): 258-260

Davis, MH; Lutzen, J; Davis, ME (2007) The spread of *Styela clava* Herdman, 1882 (Tunicata, Ascidiacea) in European waters. Aquatic Invasions 2(4): 378-390

Deudero, S; Frau, A; Cerda, M; Hampel, H (2005) Distribution and densities of the decapod crab *Percnon gibbesi*, an invasive Grapsidae, in western Mediterranean waters. Marine Ecology-Progress Series 285: 151-156

Diederich, S (2006) High survival and growth rates of introduced Pacific oysters may cause restrictions on habitat use by native mussels in the Wadden Sea. Journal of Experimental Marine Biology and Ecology 328: 211-227

Dijkstra, J; Harris, LG; Westerman, E (2007a) Distribution and long-term temporal patterns of four invasive colonial ascidians in the Gulf of Maine. Journal of Experimental Marine Biology and Ecology 342: 61-68

Dijkstra, J; Sherman, H; Harris, LG (2007b) The role of colonial ascidians in altering biodiversity in marine fouling communities. Journal of Experimental Marine Biology and Ecology 342: 169-171

Dogan, A; Onen, M; Ozturk, B (2007) A new record of the invasive Red Sea mussel *Brachidontes pharaonis* (Fischer P., 1870) (Bivalvia: Mytilidae) from the Turkish coasts. Aquatic Invasions 2(4): 461-463

Dunstan, PK; Johnson, CR (2004) Invasion rates increase with species richness in a marine epibenthic community by two mechanisms. Oecologia 138: 285-292

Eastwood, M.M., Donahue, M.J. & Fowler, A.E. (2007) Reconstructing past biological invasions: niche shifts in response to invasive predators and competitiors. Biological Invasions 9: 397-407

Edgar, GJ; Barrett, NS; Morton, AJ; Samson, CR (2004) Effects of algal canopy clearance on plant, fish and macroinvertebrate communities on eastern Tasmanian reefs. Journal of Experimental Marine Biology and Ecology 312: 67-87

Erlandsson, J; Pal, P; McQuaid, CD (2006) Re-colonisation rate differs between co-existing indigenous and invasive intertidal mussels following major disturbance. Marine Ecology-Progress Series 320: 169-176

Forrest, BM; Taylor, MD (2002) Assessing invasion impact: survey design considerations and implications for management of an invasive marine plant. Biological Invasions 4: 375-386

Gerard, VA; Cerrato, RM; Larson, AA (1999) Potential impacts of a western Pacific grapsid crab on intertidal communities of the northwestern Atlantic Ocean. Biological Invasions 1: 353-361

Gittenberger, A (2007) Recent population expansions of non-native ascidians in The Netherlands. Journal of Experimental Marine Biology and Ecology 342: 122-126

Glasby, T.M, Connell, S.D., Holloway, M.G. & Hewitt, C.L. (2007) Nonindigenous biota on artificial structures: could habitat creation facilitate biological invasions? . Marine Biology 151(3): 887-895

Grosholz, E (2001) Small spatial-scale differentiation among populations of an introduced colonial invertebrate. Oecologia 129: 58-64

Grosholz, ED; Ruiz, GM; Dean, CA; Shirley, KA; Maron, JL; Connors, PG (2000) The impacts of a nonindigenous marine predator in a California bay. Ecology 81(5): 1206-1224

Gust, N. & Inglis, G.J. (2006) Adaptive multi-scale sampling to determine an invasive crab's habitat usage and range in New Zealand. Biological Invasions 8: 339-353

Harries, DB; Harrow, S; Wilson, JR; Mair, JM; Donnan, DW (2007) The establishment of the invasive alga *Sargassum muticum* on the west coast of Scotland: a preliminary assessment of community effects. Journal of the Marine Biological Association of the United Kingdom 87: 1057-1067

Harris, L.G. & Jones, A.C. (2005) Temperature, herbivory and epibiont acquisition as factors controlling the distribution and ecological role of an invasive seaweed. Biological Invasions 7: 913-924

Harris, L.G. & Tyrrell, M.C. (2001) Changing community states in the Gulf of Maine: synergism between invaders, overfishing and climate change. Biological Invasions 3: 9-21

Hewitt, C.L., Campbell, M.L., McEnnulty, F., Moore, K.M., Murfet, N.B., Robertson, B. and Schaffelke, B. (2005) Efficacy of physical removal of a marine pest: the introduced kelp *Undaria pinnatifida* in a Tasmanian Marine Reserve. Biological Invasions 7: 251-263

Hicks, DW; Tunnell, JW; McMahon, RF (2001) Population dynamics of the nonindigenous brown mussel *Perna perna* in the Gulf of Mexico compared to other world-wide populations. Marine Ecology-Progress Series 211: 181-192

Hidalgo, F.J., Baron, P.J. and Orensanz, J.M. (2005) A prediction come true: the green crab invades the Patagonian coast. Biological Invasions 7: 547-552

Hollebone, AL; Hay, ME (2007) Propagule pressure of an invasive crab overwhelms native biotic resistance. Marine Ecology-Progress Series 342: 191-196

Holloway, M.G. and Keough, M.J. (2002a) An introduced polychaete affects recruitment and larval abundance of sessile invertebrates. Ecological Applications 12(6): 1803-1823

Holloway, MG; Keough, MJ (2002b) Effects of an introduced polychaete, *Sabella spallanzanii*, on the development of epifaunal assemblages. Marine Ecology-Progress Series 236: 137-154

Jensen, GC; McDonald, PS; Armstrong, DA (2002) East meets west: competitive interactions between green crab *Carcinus maenas,* and native and introduced shore crab *Hemigrapsus* spp.. Marine Ecology-Progress Series 225: 251-262

Jewett, EB; Hines, AH; Ruiz, GM (2005) Epifaunal disturbance by periodic low levels of dissolved oxygen: native vs. invasive species response. Marine Ecology-Progress Series 304: 31-44

Johnson, SB; Geller, JB (2006) Larval settlement can explain the adult distribution of *Mytilus californianus* Conrad but not of *M-galloprovincialis* Lamarck or *M-trossulus* Gould in Moss Landing, central California: Evidence from genetic identification of spat. Journal of Experimental Marine Biology and Ecology 328: 136-145

Kado, R (2003) Invasion of Japanese shores by the NE Pacific barnacle *Balanus glandula* and its ecological and biogeographical impact. Marine Ecology-Progress Series 249: 199-206

Kambouroglou, Nicolaidou (2006) A new alien species in Hellenic waters: *Pseudonereis anomala* (Polychaeta, Nereididae) invades harbors in the Eastern Mediterranean. Aquatic Invasions 1(2): 97-98

Klein, J; Ruitton, S; Verlaque, M; Boudouresque, CF (2005) Species introductions, diversity and disturbances in marine macrophyte assemblages of the northwestern Mediterranean Sea. Marine Ecology-Progress Series 290: 79-88

Klinger, T., Padilla, D.K., Britton-Simmons, K. (2006) Two invaders achieve higher densities in reserves. Aquatic Conservation in Marine and Freshwater Ecosystems 16: 301-311

Kraan, S; Barrington, KA (2005) Commercial farming of *Asparagopsis armata* (Bonnemaisoniceae, Rhodophyta) in Ireland, maintenance of an introduced species?. Journal of Applied Phycology 17: 103-110

Krone, R; Wanke, C; Schroder, A (2007) A new record of *Styela clava* Herdman, 1882 (Urochordata, Ascidiacea) from the central German Bight. Aquatic Invasions 2(4): 442-444

Laine, AO; Mattila, J; Lehikoinen, A (2006) First record of the brackish water dreissenid bivalve *Mytilopsis leucophaeata* in the nothern Baltic Sea. Aquatic Invasions 1(1): 38-41

Lambert, C. (2004) The south temperate and Antarctic ascidian *Corella eumyota* reported in two harbours in north-western France. Journal of the Marine Biological Association of the United Kingdom 84: 239-241

Lambert, CC; Lambert, G (1998) Non-indigenous ascidians in southern California harbors and marinas. Marine Biology 130: 675-688

Lambert, CC; Lambert, G (2003) Persistence and differential distribution of nonindigenous ascidians in harbors of the Southern California Bight. Marine Ecology-Progress Series 259: 145-161

Lambert, G (2005) First North American record of the ascidian *Perophora japonica*. Journal of the Marine Biological Association of the United Kingdom 85: 1011-1012

Lawson, J; Davenport, J; Whitaker, A (2004) Barnacle distribution in Lough Hyne Marine Nature Reserve: a new baseline and an account of invasion by the introduced Australasian species *Elminius modestus* Darwin. Estuarine, Coastal and Shelf Science 60: 729-735

Levin, P.S., Coyer, J.A., Petrik, R. and Good T.P. (2002) Community-wide effects of nonindigenous species on temperate rocky reefs. Ecology 83 (11): 3182-3193

Lewis, J.A., Watson, C., ten Hove, H.A. (2006) Establishment of the Caribbean serpulid tubeworm *Hydroides sanctaecrucis* Kroyer (in) Morch, 1863, in northern Australia. Biological Invasions 8: 665-671

Lohrer, AM; Fukui, Y; Wada, K; Whitlatch, RB (2000b) Structural complexity and vertical zonation of intertidal crabs, with focus on habitat requirements of the invasive Asian shore crab, *Hemigrapsus sanguineus* (de Haan). Journal of Experimental Marine Biology and Ecology 244: 203-217

Lohrer, AM; Whitlatch, RB (2002a) Interactions among aliens: Apparent replacement of one exotic species by another. Ecology 83(3): 719-732

Lohrer, AM; Whitlatch, RB (2002b) Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. Marine Ecology-Progress Series 227: 135-144

Lohrer, AM; Whitlatch, RB; Wada, K; Fukui, Y (2000a) Home and away: comparisons of resource utilization by a marine species in native and invaded habitats. Biological Invasions 2: 41-57

Mann, R; Harding, JM (2000) Invasion of the North American Atlantic coast by a large predatory Asian mollusc. Biological Invasions 2: 7-22

Mann, R; Harding, JM; Westcott, E (2006) Occurrence of imposex and seasonal patterns of gametogenesis in the invading veined rapa whelk *Rapana venosa* from Chesapeake Bay, USA. Marine Ecology-Progress Series 310: 129-138

Martel, C; Guarini, JM; Blanchard, G; Sauriau, PG; Trichet, C; Robert, S; Garcia-Meunier, P (2004) Invasion by the marine gastropod *Ocinebrellus inornatus* in France. III. Comparison of biological traits with the resident species *Ocenebra erinacea*. Marine Biology 146: 93-102

McDonald, J (2004) The invasive pest species *Ciona intestinalis* (Linnaeus, 1767) reported in a harbour in southern Western Australia. Marine Pollution Bulletin 49: 868-870

McDonald, PS; Jensen, GC; Armstrong, DA (2001) The competitive and predatory impacts of the nonindigenous crab *Carcinus maenas* (L.) on early benthic phase Dungeness crab *Cancer magister* Dana. Journal of Experimental Marine Biology and Ecology 258 (1): 39-54

McQuaid, CD; Phillips, TE (2000) Limited wind-driven dispersal of intertidal mussel larvae: in situ evidence from the plankton and the spread of the invasive species *Mytilus galloprovincialis* in South Africa. Marine Ecology-Progress Series 201: 211-220

Meinesz, A; Belsher, T; Thibaut, T; Antolic, B; Mustapha, KB; Boudouresque, C-F; Ciaverina, D; Cinelli, F; Cottalorda, J-M; Djellouli, A; El Abed, A; Orestano, C; Grau, AM; Ivesa, L; Jaklin, A; Langar, H; Massuti-Pascual, E; Peirano, A; Tunesi, L; de Vaugelas, J; Zavodnik, N; Zuljevic, A (2001) The introduced green alga *Caulerpa taxifolia* continues to spread in the Mediterranean. Biological Invasions 3: 201-210

Minchin, D (2007) Rapid coastal survey for targeted alien species associated with floating pontoons in Ireland. Aquatic Invasions 2(1): 63-70

Minchin, D; Davis, MH; Davis, ME (2006) Spread of the Asian tunicate *Styela clava* Herdman, 1882 to th eeast and south-west coasts of Ireland. Aquatic Invasions 1(2): 91-96

Minchin, D; Sides, E (2006) Appearance of a cryptogenic tunicate, a *Didemnum* sp fouling marina pontoons and leisure craft in Ireland. Aquatic Invasions 1(3): 143-147

Neill, P.E., Alcalde, O., Faugeron, S., Navarrete, S.A. & Correa, J.A. (2006) Invasion of *Codium fragile* ssp. *tomentosoides* in northern Chile: a new threat for *Gracilaria* farming. Aquaculture 259: 202-210

Neves, C.S., Rocha, R.M., Pitombo, F.B. & Roper, J.J. (2007) Use of artificial substrata by introduced and cryptogenic marine species in Paranagua Bay, southern Brazil. Biofouling 23(5): 319-330

Obenat, S; Spivak, E; Garrido, L (2006) Life history and reproductive biology of the invasive amphipod *Melita palmata* (Amphipoda : Melitidae) in the Mar Chiquita coastal lagoon, Argentina. Journal of the Marine Biological Association of the United Kingdom 86: 1381-1387

Occhipinti Ambrogi, A (2000) Biotic invasions in a Mediterranean Lagoon. Biological Invasions 2: 165-176

Osman, RW; Whitlatch, RB (2007) Variation in the ability of *Didemnum* sp to invade established communities. Journal of Experimental Marine Biology and Ecology 342: 40-53

Page, HM; Dugan, JE; Culver, CS; Hoesterey, JC (2006) Exotic invertebrate species on offshore oil platforms. Marine Ecology-Progress Series 325: 101-107

Page, HM; Dugan, JE; Schroeder, DM; Nishimoto, MM; Love, MS; Hoesterey, JC (2007) Trophic links and condition of a temperate reef fish: comparisons among offshore oil platform and natural reef habitats. Marine Ecology-Progress Series 344: 245-256

Pedersen, M.F., Staehr, P.A., Wernberg, T. & Thomsen M.S. (2005) Biomass dynamics of exotic *Sargassum muticum* and native *Halidrys siliquosa* in Limfjorden, Denmark- Implications of species replacements on turnover rates. Aquatic Botany 83: 31-47

Piazzi, L. and Ceccherelli, G. (2006) Persistence of biological invasion effects: recovery of macroalgal assemblages after removal of *Caulerpa racemosa* var. *cylindracea*. Estuarine, Coastal and Shelf Science 68: 455-461

Piazzi, L., Balata, D., Ceccherelli, G., Cinelli, F. (2005) Interactive effect of sedimentation and *Caulerpa racemosa* var. *cyclindracea* invasion on macroalgal assemblages in the Mediterranean Sea. Estuarine, Coastal and Shelf Science 64: 467-474

Piazzi, L; Ceccherelli, G (2002) Effects of competition between two introduced *Caulerpa*. Marine Ecology-Progress Series 225: 189-195

Piazzi, L; Ceccherelli, G; Cinelli, F (2001) Threat to macroalgal diversity: effects of the introduced green alga *Caulerpa racemosa* in the Mediterranean. Marine Ecology-Progress Series 210: 149-159

Plouguerne, E., Le Lann, K., Connan, S., Jechoux, G., Deslandes, E. & Stiger-Pouvreau, V. (2006) Spatial and seasonal variation in density, reproductive status, length and phenolic content of the invasive brown macroalga *Sargassum muticum* (Yendo) Fensholt along the coast of West Brittany (France). Aquatic Botany 85: 337-344

Porri, F; Zardi, GI; McQuaid, CD; Radloff, S (2007) Tidal height, rather than habitat selection for conspecifics, controls settlement in mussels. Marine Biology 152: 631-637

Rajbanshi, R; Pederson, J (2007) Competition among invading ascidians and a native mussel. Journal of Experimental Marine Biology and Ecology 342: 163-165

Rilov, G; Gasith, A; Benayahu, Y (2002) Effect of an exotic prey on the feeding pattern of a predatory snail. Marine Environmental Research 54(1): 85-98

Rius, M; McQuaid, CD (2006) Wave action and competitive interaction between the invasive mussel Mytilus galloprovincialis and the indigenous *Perna perna* in South Africa. Marine Biology 150: 69-78

Rivest, BR; Coyer, J; Tyler, S (1999) The first known invasion of a free-living marine flatworm. Biological Invasions 1: 393-394

Robinson, TB; Branch, GM; Griffiths, CL; Govender, A; Hockey, PAR (2007) Changes in South African rocky intertidal invertebrate community structure associated with the invasion of the mussel *Mytilus galloprovincialis*. Marine Ecology-Progress Series 340: 163-171

Roche, DG; Torchin ME (2007) Established population of the North American Harris mud crab, *Rhithropanopeus harrisii* (Gould 1841) (Crustacea: Brachyura: Xanthidae) in the Panama Canal. Aquatic Invasions 2(3): 155-161

Rueness, J; Heggoy, E; Husa, V; Sjotun, K (2007) First report of the Japanese red alga *Antithamnion nipponicum* (Ceramiales, Rhodophyta) in Norway, an invasive species new to northern Europe. Aquatic Invasions 2(4): 431-434

Ruesink, JL (2007) Biotic resistance and facilitation of a non-native oyster on rocky shores. Marine Ecology-Progress Series 331: 1-9

Ruitton, S; Javel, F; Culioli, JM; Meinesz, A; Pergent, G; Verlaque, M (2005) First assessment of the *Caulerpa racemosa* (Caulerpales, Chlorophyta) invasion along the French Mediterranean coast. Marine Pollution Bulletin 50: 1061-1068

Sanchez, I; Fernandez, C (2006) Resource availability and invasibility in an intertidal macroalgal assemblage. Marine Ecology-Progress Series 313: 85-94

Saunders, M; Metaxas, A (2007) Temperature explains settlement patterns of the introduced bryozoan *Membranipora membranacea* in Nova Scotia, Canada. Marine Ecology-Progress Series 344: 95-106

Scheibling, RE; Gagnon, P (2006) Competitive interactions between the invasive green alga *Codium fragile* ssp *tomentosoides* and native canopy-forming seaweeds in Nova Scotia (Canada). Marine Ecology-Progress Series 325: 1-14

Schmidt, AL; Scheibling, RE (2007) Effects of native and invasive macroalgal canopies on composition and abundance of mobile benthic macrofauna and turf-forming algae. Journal of Experimental Marine Biology and Ecology 341: 110-130

Schneider, KR; Helmuth, B (2007) Spatial variability in habitat temperature may drive patterns of selection between an invasive and native mussel species. Marine Ecology-Progress Series 339: 157-167

Schwindt, E (2007) The invasion of the acorn barnacle *Balanus glandula* in the south-western Atlantic 40 years later. Journal of the Marine Biological Association of the United Kingdom 87: 1219-1225

Schwindt, E; Bortolus, A; Iribarne, OO (2001) Invasion of a reef-builder polychaete: direct and indirect impacts on the native benthic community structure. Biological Invasions 3: 137-149

Sebastian, CR; Steffani, CN; Branch, GM (2002) Homing and movement patterns of a South African limpet *Scutellastra argenvillei* in an area invaded by an alien mussel *Mytilus galloprovincialis*. Marine Ecology-Progress Series 243: 111-122

Sezgin, M; Aydemir, E; Ates, AS; Katagan, T; Ozcan, T (2007) On the presence of the non-native estuarine shrimp, *Palaemon longirostris* H.Milne-Edwards, 1837 (Decapoda, Caridea), in the Black Sea. Aquatic Invasions 2(4): 464-465

Silva, PC; Woodfield, RA; Cohen, AN; Harris, LH; Goddard, JHR (2002) First report of the Asian kelp *Undaria pinnatifida* in the northeastern Pacific Ocean. Biological Invasions 4: 333-338

Simkanin, C; Power, A; Myers, A; McGrath, D; Southward, A; Mieszkowska, N; Leaper, R; O'Riordan, R (2005) Using historical data to detect temporal changes in the abundances of intertidal species on Irish shores. Journal of the Marine Biological Association of the United Kingdom 85: 1329-1340

Simon, C; Gall, EA; Deslandes, E (2001) Expansion of the red alga *Grateloupia doryphora* along the coasts of Brittany (France). Hydrobiologia 443: 23-29

Smith, LD (2004) Biogeographic differences in claw size and performance in an introduced crab predator *Carcinus mamas*. Marine Ecology-Progress Series 276: 209-222

Stachowicz, J.J., Fried, H., Osman, R.W. and Whitlatch, R.B. (2002a) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology 83(9): 2575-2590

Stachowicz, JJ; Terwin, JR; Whitlatch, RB; Osman, RW (2002b) Linking climate change and biological invasions: Ocean warming facilitates nonindigenous species invasions.

Proceedings of the National Academy of Sciences of the United States of America 99: 15497-15500

Stachowicz, JJ; Whitlatch, RB; Osman, RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286: 1577-1579

Staehr, PA; Pedersen, MF; Thomsen, MS; Wernberg, T; Krause-Jensen, D (2000) Invasion of *Sargassum muticum* in Limfjorden (Denmark) and its possible impact on the indigenous macroalgal community. Marine Ecology-Progress Series 207: 79-88

Steffani, CN; Branch, GM (2003) Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. Marine Ecology-Progress Series 246: 197-209

Steffani, CN; Branch, GM (2005) Mechanisms and consequences of competition between an alien mussel, *Mytilus galloprovincialis*, and an indigenous limpet, *Scutellastra argenvillei*. Journal of Experimental Marine Biology and Ecology 317: 127-142

Strong, JA; Dring, MJ; Maggs, CA (2006) Colonisation and modification of soft substratum habitats by the invasive macroalga *Sargassum muticum*. Marine Ecology-Progress Series 321: 87-97

Sumi, CBT; Scheibling, RE (2005) Role of grazing by sea *urchins Strongylocentrotus droebachiensis* in regulating the invasive alga *Codium fragile* ssp *tomentosoides* in Nova Scotia. Marine Ecology-Progress Series 292: 203-212

Thibaut, T., Meinesz, A., Coquillard, P. (2004) Biomass seasonality of *Caulerpa taxifolia* in the Mediterranean Sea. Aquatic Botany 80: 291-297

Thieltges, DW (2005) Impact of an invader: epizootic American slipper limpet *Crepidula fornicata* reduces survival and growth in European mussels. Marine Ecology-Progress Series 286: 13-19

Thieltges, DW; Strasser, M; van Beusekom, JEE; Reise, K (2004) Too cold to prosper - winter mortality prevents population increase of the introduced American slipper limpet *Crepidula fornicata* in northern Europe. Journal of Experimental Marine Biology and Ecology 311: 375-391

Thornber, CS; Kinlan, BP; Graham, MH; Stachowicz, JJ (2004) Population ecology of the invasive kelp *Undaria pinnatifida* in California: environmental and biological controls on demography. Marine Ecology-Progress Series 268: 69-80

Torchin, ME; Lafferty, KD; Kuris, AM (2001) Release from parasites as natural enemies: increased performance of a globally introduced marine crab. Biological Invasions 3: 333-345

Tsai, ML; Dai, CF (2001) Life history plasticity and reproductive strategy enabling the invasion of *Ligia exotica* (Crustacea : Isopoda) from the littoral zone to an inland creek. Marine Ecology-Progress Series 210: 175-184

Tsiamis, K; Panayotidis, P (2007) First record of the red alga *Asparagopsis taxiformis* (Delile) Trevisan de Saint-Leon in Greece. Aquatic Invasions 2(4): 435-438

Tyrrell, M.C. & Byers, J.E. (2007) Do artifical substrates favor nonindigenous fouling species over native species? Journal of Experimental Marine Biology and Ecology 342: 54-60

Valentine, JP; Johnson, CR (2003) Establishment of the introduced kelp *Undaria pinnatifida* in Tasmania depends on disturbance to native algal assemblages. Journal of Experimental Marine Biology and Ecology 295: 63-90

Valentine, JP; Johnson, CR (2005) Persistence of the exotic kelp *Undaria pinnatifida* does not depend on sea urchin grazing. Marine Ecology-Progress Series 285: 43-55

Viejo, R.M. (1999) Mobile epifauna inhabitating the invasive *Sargassum muticum* and two local seaweeds in northern Spain. Aquatic Botany 64: 131-149

Wason, K., Fenn, K. & Pearse, J.S. (2005) Habitat differences in marine invasions of central California. Biological Invasions 7: 935-948

Wasson, K., Zabin, C.J., Bedinger, L., Diaz, M.C. & Pearse, J.S. (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biological Conservation 102: 143-153

Watson, D.I., O'Riordan, R.M., Barnes, D.K.A. and Cross, T. (2005) Temporal and spatial variability in the recruitment of barnacles and the local dominance of *Elminius modestus* Darwin in SW Ireland. Estuarine, Coastal and Shelf Science 63: 119-131

White, LF; Shurin, JB (2007) Diversity effects on invasion vary with life history stage in marine macroalgae. Oikos 116: 1193-1203

Wikstrom, S.A. & Kautsky, L. (2004) Invasion of a habitat forming seaweed: effects on associated biota. Biological Invasions 6: 141-150

Wikstrom, SA; Pavia, H (2004) Chemical settlement inhibition versus post-settlement mortality as an explanation for differential fouling of two congeneric seaweeds. Oecologia 138: 223-230

Willis, KJ; Cook, EJ; Lozano-Fernandez, M; Takeuchi, I (2004) First record of the alien caprellid amphipod, *Caprella mutica*, for the UK. Journal of the Marine Biological Association of the United Kingdom 84: 1027-1028

Wright, J.T. and Davis, A.R. (2006) Demographic feedback between clonal growth and fragmentation in an invasive seaweed. Ecology 87(7): 1744-1754

Wyatt, A.S.J., Hewitt, C.L., Walker, D.I. and Ward, T.J. (2005) Marine introductions in the Shark Bay World Heritage Property, Western Australia: a preliminary assessment. Diversity and Distributions 11: 33-44

Yokes, B; Galil, B.S. (2006) The first record of the needle-spined urchin *Diadema setosum* (Leske, 1778) (Echinodermata: Echinoidea: Diadematidae) from the Mediterranean Sea. Aquatic Invasions 1(3): 188-190

Yokes, B; Galil, BS (2006) Touchdown-first record of *Percnon gibbesi* (H. Milne Edwards, 1853) (Crustacea: Decapoda: Grapsidae) from the Levantine coast. Aquatic Invasions 1(3): 130-132

Yokes, MB; Karhan, SU; Okus, E; Yuksek, A; Aslan-Yilmaz, A; Yilmaz, IN; Demirel, N; Demir, V; Galil, B.S. (2007) Alien crustacean decapods from the Aegean Coast of Turkey. Aquatic Invasions 2(3): 162-168

Zabin, C.A., Zardus, J., Pitombo, F.B., Fread, V. & Hadfield, M.G. (2007) A tale of three seas: consistency of natural history traits in a Caribbean-Atlantic barnacle introduced to Hawaii. Biological Invasions 9: 523-544

Zabin, CJ; Altieri, A (2007) A Hawaiian limpet facilitates recruitment of a competitively dominant invasive barnacle. Marine Ecology-Progress Series 337: 175-185

Zaiko, A., Olenin, S., Daunys, D. & Nalepa, T. (2007) Vulnerability of benthic habitats to the aquatic invasive species. Biological Invasions 9(6): 703-714

Zardi, GI; McQuaid, CD; Nicastro, KR (2007) Balancing survival and reproduction: seasonality of wave action, attachment strength and reproductive output in indigenous *Perna perna* and invasive *Mytilus galloprovincialis* mussels. Marine Ecology-Progress Series 334: 155-163

Zardi, GI; Nicastro, KR; McQuaid, CD; Rius, M; Porri, F (2006) Hydrodynamic stress and habitat partitioning between indigenous (*Perna perna*) and invasive (*Mytilus galloprovincialis*) mussels: constraints of an evolutionary strategy. Marine Biology 150: 79-88

Zuljevic, A; Antolic, B; Onofri, V (2003) First record of *Caulerpa racemosa* (Caulerpales : Chlorophyta) in the Adriatic Sea. Journal of the Marine Biological Association of the United Kingdom 83: 711-712