MARINE INVASIVE SPECIES

STATE OF THE GULF OF MAINE REPORT

Gulf of Maine Council on the Marine Environment

June 2010

MARINE INVASIVE SPECIES

STATE OF THE GULF OF MAINE REPORT

TABLE OF CONTENTS

Gulf of Maine Council on the Marine Environment

MASSACHUSETTS OFFICE OF COASTAL ZONE MANAGEMENT

This publication was made possible through the support of the Gulf of Maine Council on the Marine Environment and the Massachusetts Office of Coastal Zone Management.

The Gulf of Maine Council on the Marine Environment was established in 1989 by the Governments of Nova Scotia, New Brunswick, Maine, New Hampshire and Massachusetts to foster cooperative actions within the Gulf watershed. Its mission is to maintain and enhance environmental quality in the Gulf of Maine to allow for sustainable resource use by existing and future generations.

Cover photo (lionfish) by Jens Petersen

Cover map (background) courtesy of Census of Marine Life/Gulf of Maine Area Program

CONTRIBUTORS

AUTHOR:
Adrienne Pappal
Massachusetts Office of Coastal Zone Management
Aquatic Invasive Species Program
251 Causeway St., Suite 800
Boston MA, 02114

EDITORIAL COMMITTEE:
Jay Walmsley, Editor-in-Chief, Fisheries and Oceans Canada
Paul Currier, New Hampshire Department of Environmental Services
Diane Gould, US Environmental Protection Agency
Liz Hertz, Maine State Planning Office
Justin Huston, Nova Scotia Department of Fisheries and Aquaculture
Michele L. Tremblay, naturesource communications, Gulf of Maine Council on the Marine Environment

DESIGN AND LAYOUT:
Waterview Consulting, www.waterviewconsulting.com

1. Issue in Brief

Marine habitats in the Gulf of Maine support an ever-growing suite of marine invasive species, defined as non-native species that cause or are likely to cause harm to ecosystems, economies, and/or public health (ISAC 2006). Invading marine species were first introduced to the northwest Atlantic region by early explorers, either purposely for food sources or accidentally through fouling on the hulls of wooden ships and other means. In modern times, there are a wide variety of transfer mechanisms (vectors) available for hitchhiking marine invaders to travel and spread. At least 64 invasions have occurred in the Gulf of Maine ecosystem, and more are likely to be discovered. Pressures such as habitat modification, aquaculture, shipping, and climate change will continue to have unintended impacts on the system and further influence the survival of non-native species (Figure 1). Impacts from marine invasive species in the Gulf of Maine vary from competitive displacement of native species to aesthetic impacts and fouling of gear, although there is little empirical evidence available, particularly for economics, to assess impacts in depth. Management of invading species in the marine environment is a relatively new endeavour, and there is much to learn regarding successful prevention and control of organisms in open systems. Current regulatory responses are moving toward a more effective management approach that includes a focus on early detection, rapid response, research, and education. These efforts will go a long way in helping to understand the impacts of marine invasive species and protect Gulf of Maine ecosystems and economies.

LINKAGES

This theme paper also links to the following theme papers:

- Climate Change and Its Effects on Ecosystems, Habitats, and Biota
- Species at Risk
- Coastal Ecosystems and Habitats
- Emerging Issues

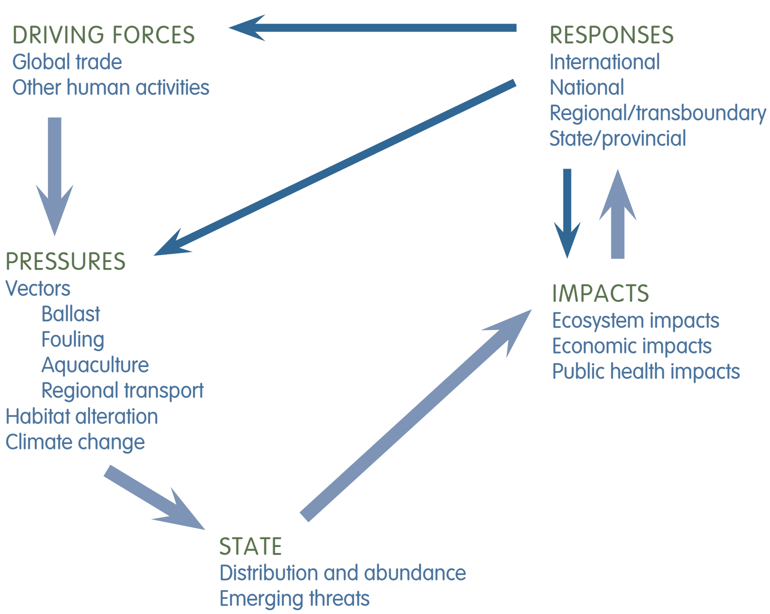

Figure 1: Driving forces, pressures, state, impacts and responses (DPSIR) to marine invasive species in the Gulf of Maine. The DPSIR framework provides an overview of the relation between the environment and humans. According to this reporting framework, social and economic developments and natural conditions (driving forces) exert pressures on the environment and, as a consequence, the state of the environment changes. This leads to impacts on human health, ecosystems and materials, which may elicit a societal or government response that feeds back on all the other elements.

2. Driving Forces and Pressures

Driving forces are factors that lead to environmental change. Pressures on the environment stem from these driving forces, resulting in changes to the quality or condition of the ecosystem (see Figure 1). The primary driving force behind marine introductions is the transportation, trade practices, and other activities of humans. Transport mechanisms, or vectors, associated with human activity include transport of species within or on ships, aquaculture, intentional introductions, and trade (pet trade, live seafood). In addition, other pressures such as habitat modification and climate change alter the survival rates of both native and non-native species and may influence establishment of marine invaders.

2.1 GLOBAL TRADE AND EXPLORATION

Humans have introduced marine species to new environments inadvertently, and at times purposely, for centuries (Carlton 1996a). The rise in global trade through commercial shipping in particular has dissolved historical barriers for distribution of marine organisms and has led to an unprecedented increase in the rate of marine introductions in the last 200 years (Carlton 1985; Ruiz et al. 2000a). In the Gulf of Maine, the majority of marine invaders originate from Europe (Figure 2), highlighting the importance of global trading routes between the northeast and northwest Atlantic in marine introductions (Pederson et al. 2005). Commercial shipping has led to the introduction of marine invasive species into the Gulf of Maine through two primary mechanisms: transport by ballast and fouling on ship surfaces (hull, sea chest, etc.) (Table 1).

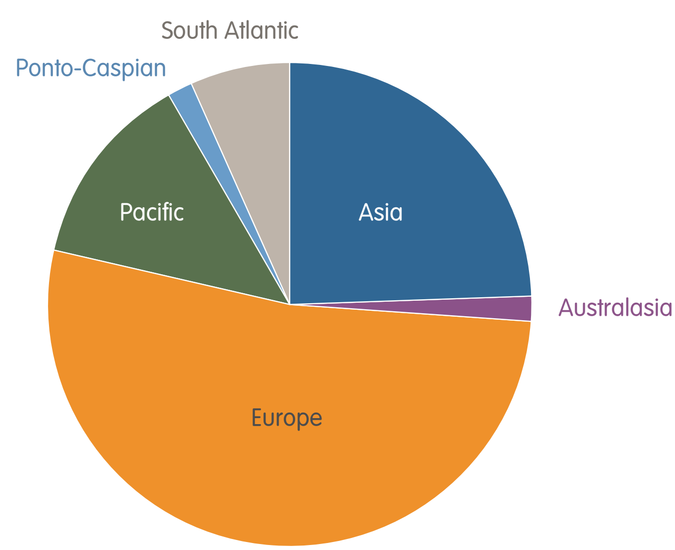

Figure 2: Origin of marine invasive species in the Gulf of Maine.

Sources: Ford 1996; Schwaninger 1999; Hayward et al. 2001; Gavio and Fredericq 2002; Carlton 2003; Carlton 2004; Mathieson et al. 2008a; Mathieson et al. 2008b; Brawley et al. 2009

Table 1: Species introduced by shipping in the Gulf of Maine.

SPECIES	VECTOR	SOURCE
Furcellaria lumbricalis (red alage)	Ballast Water	Mathieson et al. 2008c
Ovatella mysotis (mouse ear snail)	Rock Ballast	Carlton 1992
Fucus serratus (brown algae)	Rock Ballast	Brawley et al. 2009
Littorina littorea (common periwinkle)	Rock Ballast	Brawley et al. 2009
Neosiphonia harveyi (red algae)	Fouling	Mathieson et al. 2008c
Porphyra katadae (nori, red algae)	Fouling	Mathieson et al. 2008c
Botryllus schlosseri (star tunicate)	Fouling	Dijkstra et al. 2007a
Diplosoma listerianum (tunicate)	Fouling	Dijkstra et al. 2007a
Codium fragile ssp *fragile* (green fleece)	Fouling	Carlton and Scanlon 1985
Antithamnion pectinatum (red algae)	Shipping, unspecified	Mathieson et al. 2008c
Bonnemaisonia hamifera (red algae)	Shipping, unspecified	Mathieson et al. 2008b
Lomentaria clavellosa (red algae)	Shipping, unspecified	Mathieson et al. 2008b
Melanosiphon intestinalis (brown algae)	Shipping, unspecified	Mathieson et al. 2008b
Convoluta convoluta (flatworm)	Shipping, unspecified	Rivest et al. 1999

2.1.1 Ballast

The use of solid ballast obtained from intertidal habitats of Europe may have transported entire communities to the Gulf of Maine, and has been implicated in the introduction and subsequent spread of the brown algae *Fucus serratus* and snail *Littorina littorea* to Nova Scotia in the 18th Century (Carlton 1996b; Brawley et al. 2009). In the last half century, an increased number of commercial vessels, reduction of toxins in ballast water, and larger capacity of ballast tanks have improved the survival of marine invaders in transit and thus the number of viable marine introductions (Carlton 1985; Carlton 1996b; Cohen and Carlton 1998). Mysids, amphipods, cladocerans, copepods, numerous microscopic planktonic organisms, algal filaments, and fish have been observed to survive in ballast tanks in journeys lasting nearly two weeks, while polychaete larvae and copepods can survive voyages of 30 days or more (Carlton 1985). In the Gulf of Maine, it is hypothesized that the red alga *Furcellaria lumbricalis* was introduced via ballast water (Mathieson et al. 2008a).

Photo: Jim Frazier

2.1.2 Fouling

Fouling is the accumulation of marine organisms on the hull, sea chest, and other surfaces of ships. Distinguishing between introductions resulting from fouling versus ballast water is extremely difficult (Carlton 1985). However, species that have short-lived larvae, which are not likely to survive long journeys in ballast water, are candidates for introductions through fouling (Carlton and Geller 1993). For example, in the Gulf of Maine it is hypothesized that the colonial tunicates *Botrylloides violaceus* and *Diplosoma listerianum* were fouling introductions due, in part, to their short larval period (Dijkstra et al. 2007a). Modern vessels are faster, have shorter times in port, and are more frequently maintained, thus the role of hull fouling in recent transoceanic introductions has been questioned (Carlton and Hodder 1995). However, Drake and Lodge (2007) recently collected close to 1,000 live organisms from the hull of a single cargo ship entering the Great Lakes from Algeria, indicating that the importance of this vector should not be overlooked. There are at least five species in the Gulf of Maine that may have been introduced by fouling (see Table 1).

2.2 PRESSURES FROM OTHER HUMAN ACTIVITIES

The high concentration of people living on the coast and their associated economic and social activities results in numerous pathways (vectors) that can facilitate the regional spread of marine introduced species. For example, transport of species for aquaculture is implicated in several marine introductions in the Gulf of Maine. Recreational boating and other related activities transport marine invaders from their point of introduction to additional areas, while anthropogenic disturbances to coastal habitats, such as pollution, habitat modification, and climate change may alter survival rates and interactions of native and non-native species.

2.2.1 Aquaculture

Photo: DFO

"…but the greatest agency of all that spreads marine animals to new quarters of the world must be the business of oyster culture." – Elton 1958

Transfer of non-native species for aquaculture, particularly oysters, has been identified as a major vector of marine introductions in North America (Ruiz et al. 2000a). Species have been introduced directly to the Gulf of Maine for aquaculture purposes, as with the European oyster, *Ostrea edulis*, or may be secondarily associated with aquaculture organisms (Carlton 1992; McKindsey et al. 2007). It is hypothesized that introductions of ubiquitous and aggressive species such as the colonial tunicates *Didemnum vexillum* and *Botrylloides violaceus* and the green algae *Codium fragile* ssp. *fragile* resulted from the transfer of oysters for aquaculture (Mathieson et al. 2003; Dijkstra et al. 2007a). In nearby Prince Edward Island, regional transport of invasive tunicates stemming from the movement of bivalves for aquaculture is a known problem (Locke et al. 2007). Past import of *Anguilla rostrata* (American eel) for aquaculture led to the spread of the nematode parasite *Anguillicola crassus* throughout the Gulf of Maine (Aieta and Olivera 2009).

2.2.2 Habitat Modification

The role of habitat modification on the introduction and survival of non-native marine species in the Gulf of Maine is not clear. However, increased numbers of non-native species are often seen in areas disturbed by human activities, and successful invaders may possess traits that enable them to perform better in altered habitats relative to native species (Cohen and Carlton 1998; Byers 2002). It is thought that native species compete best on surfaces for which they are evolutionarily adapted, giving non-native species a competitive advantage on newer, artificial substrates (Tyrell and Byers 2007). For example, marine invasive species are often more likely to be present on floating pontoons and pilings than adjacent natural habitat (Glasby et al. 2007; Tyrell and Byers 2007).

Photo: N. Houlihan

Water quality conditions may also play a role in the establishment of marine invasive species. For example, the red alga *Grateloupia turuturu*, a recent invader to the Gulf of Maine, is highly tolerant of polluted waters (Farnham 1980). In eutrophic (nutrient rich) systems, invasive species that are better competitors at high nutrient levels and low oxygen conditions may have an advantage over native species (Byers 2002). However, direct relationships between survival of marine invaders and water quality are not always clear; in southern New England both native and non-native ascidians are most diverse in areas of fair water quality and moderate levels of nitrogen (Carmen et al. 2007). Ironically, recent improvements to water quality, both in local harbors and distant source ports, have been implicated in increased survival of marine invaders both in ballast and at the point of introduction (Carlton 1996a).

2.2.3 Climate Change

Climate change and the resultant modifications in habitat may impact the survival and establishment of species in various ways. Hellmann et al. (2008) propose several consequences of climate change on marine invasive species relevant to the Gulf of Maine: altered patterns of human transport (longer shipping seasons, new routes, etc.), altered climatic restraints favoring non-natives or increasing the possibility of survival for previously unsuccessful invasions, altered distributions (range shifts, etc.), and altered impacts. Long-term studies of rocky shores in California have shown latitudinal shifts in species abundance and geographic range boundaries as a result of temperature increases, and similar changes may occur in the Gulf of Maine if temperatures continue to rise (Barry et al. 1995; see Climate Change). Since organisms are generally most abundant in the center of their range, species with more southerly borders should expand, while those with northern boundaries should decrease (Barry et al. 1995). For example, a warming trend during the last mid century is implicated in the expansion of the green crab, *Carcinus maenas*, from waters south of Cape Cod Massachusetts into the Gulf of Maine (Glude 1955). Changes in climate resulting in warmer winter water temperatures in particular could provide a thermal refuge for invading species and may have important impacts to timing of recruitment and survival (Ruiz et al. 1999). For example, it is hypothesized that the degree to which the invasive tunicate *Didemnum vexillum* degrades in cold weather influences its ability to regenerate and reproduce sexually, thus an increase in winter water temperatures may enhance the reproductive capability of this species (Valentine et al. 2009). The non-native tunicates *Ascidiella aspersa*, *Botrylloides violaceus*, and *Diplosoma listerianum* recruit earlier in warmer years, and total annual recruitment is positively correlated with mean winter water temperature (Stachowicz et al. 2002). The invasive red algae *Grateloupia turuturu* produces larger blades during warm temperature events, resulting in increased cover (Harlin and Villalard-Bohnsack 2001). An increase in winter water temperatures has also been linked to a rise in *Perkinsus marinus* (Dermo disease) outbreaks in oysters (Cook et al. 1998).

2.2.4 Regional Transport for Trade and Recreation

Photo: Adrienne Pappal

Transport of marine introduced species from their point of introduction to other areas regionally can occur through many vectors. Coastwide trade (short-sea shipping) and recreational boating are likely important transport vectors throughout and between the Gulf of Maine, southern Atlantic, and northern Canada. Boat hulls, propellers, chains, anchors, and ropes are easily fouled by marine invaders, facilitating spread when the vessel relocates or is cleaned, particularly for species capable of reproducing through fragmentation, such as colonial tunicates and algae (Bégin and Scheibling 2003; Bullard et al. 2007). Domestic arrivals account for about 35 percent of the total ballast water discharged in New England, and ballast water exchange zones are located within Gulf of Maine waters for ship traffic to and from Canada (Hines et al. 2004; Transport Canada 2010). It is likely that regional transport vectors facilitated the spread of *Littorina littorea* from the Gulf of St. Lawrence to the Gulf of Maine (Brawley et al. 2009). *Perkinsus marinus*, the protozoan resulting in Dermo disease of oysters, and the barnacles *Chthamalus fragilis* and *Balanus subalbidus* all have expanded their range northward to the Gulf of Maine from south Atlantic waters, likely aided by domestic shipping vectors (Carlton 2003). The Asian shore crab, *Hemigrapsus sanguiensus*, was able to rapidly expand from its point of introduction on the New Jersey coast to as far north as Schoodic Peninsula, Maine, in only 10 years (McDermott 1991; Delaney et al. 2008).

3. Status and Trends

At least 64 marine invasive species have been documented in the Gulf of Maine (Table 2). This count does not include cryptogenic species, organisms that cannot definitively be identified as native or introduced, which are likely to comprise a significant number of species in the region (Carlton 1996b). For example, it is estimated that at least 67 cryptogenic marine species reside in the waters of Long Island Sound to Nova Scotia (Carlton 2003). This count also does not represent results from comprehensive monitoring of all habitats. The bulk of information on marine introductions in the Gulf of Maine and elsewhere is from coastal and estuarine systems, and due to logistical constraints and identification difficulties, only some habitats and taxa are adequately represented. For example, very little information is available on soft substrate benthic infauna, and various microscopic organisms are most certainly underrepresented. Additionally, the identification status for several organisms is not well defined and may fluctuate through genetic work and advanced study. For example, the invasive red algae *Neosiphonia harveyi* was misidentified as the native *Polysiphonia harveyi*

Table 2: Marine invasive species in the Gulf of Maine.

TAXONOMIC GROUP	NUMBER	SOURCE
Crustacea	13	Swan 1956; Beckman and Menzies 1960; Maurer and Wigley 1982; Larsen and Doggett 1991; Wethey 2002; Carlton 2003; Trott 2004; Pederson et al. 2005; Delaney et al. 2008
Rhodophyceae	11	Mathieson et al. 2008 a,b,c
Tunicata	7	Pederson et al. 2005; Harris and Dijkstra 2007
Mollusca	6	Carlton 1992; Carlton 2003; Pederson et al. 2005
Phaeophyceae	5	Hooper and South 1977; Mathieson et al. 2008 a,b,c
Hydrozoa	3	Smith 1964; Blezard 1999; Trott 2004
Bryozoa	3	Scheibling et al. 1999; Pederson et al. 2005
Protista	3	Ford 1996; Cook et al. 1998; Bower 2007
Cnidaria	2	Trott 2004; Pederson et al. 2005
Polychaeta	2	Carlton 2004; Pederson et al. 2005
Platyhelminthes	2	Cone and Marcogliese 1995; Rivest et al. 1999
Diatomacea	2	Carlton 2003; Martine and LeGresley 2008
Kamptozoa	1	Wasson et al. 2000
Nematoda	1	Aieta and Oliveira 2009
Porifera	1	Pederson et al. 2005
Cholorophyceae	1	Pederson et al. 2005; Mathieson et al 2008b
Virus	1	Bouchard et al. 2001
TOTAL	64	

for nearly 150 years until recent genetic work suggested otherwise (McIvor 2000; Mathieson et al. 2003; Mathieson et al. 2008 b,c).

The number and abundance of marine invasive species in the Gulf of Maine appears to be increasing, likely reflecting concurrent increases in pressures as discussed in the previous section. Introduced seaweeds in Casco Bay and the Mount Desert Region in Maine have increased 3-4.5 fold in 100 years (Mathieson et al. 2008c). Percent cover of non-native colonial ascidians has increased in the last quarter century at long-term study sites in the Gulf of Maine (Dijkstra et al. 2007a). Eight new dinoflagellete species and 14 new diatom species have been observed in the Bay of Fundy during the last 15 years, although it is unclear whether these records represent true introductions (Martine and LeGresley 2008). The abundance and dominance of marine invaders has also shifted over time. The non-native colonial ascidian *Botryllus schlosseri* was once dominant at long-term study sites in the late 1970s, where currently *Botrylloides violaceus* and *Didemnum vexillum* are the primary spatial competitors (Dijkstra et al. 2007a). *Hemigrapsus sanguineus* has begun to dominate communities once occupied by *Carcinus maenas*, likely a product of a high reproductive rate; densities of up to 40-90 *H. sanguineus* per square meter are common in Long Island Sound (Loher and Whitlatch 2002; Delany et al. 2008). Similar abundance levels can be expected in the Gulf of Maine as *H. sanguineus* continues to expand northward (Delany et al. 2008).

3.1 EMERGING THREATS

Emerging threats include marine invaders that have been recently introduced to the Gulf of Maine, introduced species that have expanded their range significantly in recent years, or species that threaten to invade the region. Since these organisms are relatively new invaders, or have not yet been introduced, their impacts and spread within the Gulf of Maine are difficult to predict. A few case studies are highlighted below.

3.1.1 *Grateloupia turuturu*


Photo: Adrienne Pappal

Grateloupia turuturu, a red alga native to Asia, was first reported in New England waters (as *G. doryphora*) in 1994 (Harlin and Villalard-Bohnsack 2001). Since introduction, *G. turuturu* has continued to expand northward and was first recorded in the Gulf of Maine in 2007 (Mathieson et al. 2008d). This species has multiple reproductive strategies and can grow rapidly, eventually leading to 100 percent cover of some study sites in Narragansett Bay, Rhode Island, during the growing season (Harlin and Villalard-Bohnsack 2001). In Mount Hope Bay, Massachusetts, total attached Rhodophyceae (red algae) accounted for less than three percent cover in the intertidal zone in 2006, and just two years later *G. turuturu* covered nearly 25 percent of the low intertidal during high growth periods (Pappal 2006; Pappal pers. obs.). Impacts from invasive seaweeds generally include competition for resources, shading, displacement, and loss of native algal biomass (Scaffelke and Hewitt 2007). Impacts of this species in the Gulf of Maine are as of yet unknown, however, *G. turuturu* has broad environmental tolerances and is likely to continue to spread into the northern Gulf of Maine (Mathieson et al. 2008d).

3.1.2 *Didemnum vexillum*

Photo: Adrienne Pappal

It is thought that the non-native colonial tunicate *Didemnum vexillum* was first introduced to the Damariscotta River area in Maine as a hitchhiker on oysters for aquaculture (Dijkstra et al. 2007a). While there have been anecdotal reports of *D. vexillum* in the Gulf of Maine since the 1970s, it is only relatively recently that this species has begun to aggressively expand its range (Bullard et al. 2007). *Didemnum vexillum* utilizes multiple reproductive strategies to facilitate its spread: it can reproduce both sexually and by fragmentation, and fragments may contain larvae that can be released upon reattachment (Bullard et al. 2007; Valentine et al. 2009). Unlike other invasive tunicates, *D. vexillum* is able to recruit to and utilize open coast and deep water habitats (Osman and Whitlach 2007). It was first recorded on Georges Bank in 2002 and by 2005 had formed large mats that covered more than 50 percent of some transects (Valentine et al. 2007). It has no known predators, and its tunic is highly acidic (Bullard et al. 2007; Valentine et al. 2007). *Didemnum vexillum* is able to overgrow and displace most species and established communities, including pebbles, cobbles, boulders, sea scallops, mussels, shells, sponges, bryozoans, hydrozoans, tube worms, and tunicates (Osman and Whitlatch 2007; Valentine et al. 2007). The formation of large colonies may influence the recruitment of other species and could form a barrier to prey and modify habitat, or lead to the death of bivalves by overgrowing their siphons (Bullard et al. 2007; Dijkstra et al. 2007b; Valentine et al. 2007). Control of aggressive ascidians invaders is difficult, and currently there are no effective means to prevent the spread of this species in the Gulf of Maine. In New Zealand, a focused control effort of *D. vexillum* was attempted, and while some methods were effective during the short term, the overall effort failed resulting in significant losses to nearby mussel farms (Coutts and Forrest 2007). *Didemnum vexillum* has not yet been recorded in Canada at the time of this writing, but has been documented near the US-Canada boundary on Georges Bank (Valentine et al. 2007, 2009).

3.1.3 *Eriocheir sinensis* (Mitten Crab)

Photo: Christian Fischer

Eriocheir sinensis has not been reported in Gulf of Maine waters to date, but has been expanding its range along the Atlantic coast since it was first detected in Maryland in 2006 (Ruiz et al. 2006). Populations of *E. sinensis* are found in bordering watersheds including the Hudson River in New York and the St. Lawrence River in Quebec (Ruiz et al. 2006; Veilleux and de Lafontaine 2007). It is a catadromous species that migrates from freshwater rivers and tributaries to reproduce in saltwater (Rudnick et al. 2005). Primary impacts include riverbank erosion from burrowing activity, clogging of intake pipes and screens, competition with native species, and human health impacts (it is an intermediate host to a parasitic lung fluke) (Rudnick et al. 2005; Ruiz et al. 2006). In the United States, *E. sinensis* is regulated as an injurious species under the Lacey Act, thus import, export, and interstate transport of this species is illegal without a permit.

3.1.4 *Pterois volitans/miles* (Lionfish)


Photo: Jens Petersen

Likely first introduced into Atlantic waters when a Florida aquarium was damaged during Hurricane Andrew in 1992, juvenile *Pterois* have now been recorded as far north as Rhode Island (Courtenay 1995, as cited in Whitfield et al. 2002; Whitfield et al. 2007). Impacts of *P. volitans/miles* include predation, competition, and displacement of native fish, and its sting can cause serious injury to humans (Hare and Whitfield 2003; Whitfield et al. 2007). Temperature is a limiting factor in the distribution of this species and it is not likely to overwinter in Gulf of Maine waters (Hare and Whitfield 2003). However, temperature increases concurrent with climate change, particularly warmer winter temperatures, may enable the future survival of *P. volitans/miles* in the Gulf of Maine.

4. Impacts

The definition of an invasive species is a non-native or cryptogenic species introduced by humans that causes harm to ecosystem or economic resources (Carlton 1996b). However, deciphering what this harm may be for a particular species is difficult, and there are relatively few empirical studies available on the impacts of invasive species (Ruiz et al. 1999; Stone and Lovell 2005; Scaffelke and Hewitt 2007). In general, historical records and pre-invasion data for most species and coastal communities are lacking, thus when an invasion occurs there is no baseline condition from which to evaluate impacts (Parker et al. 1999; Ruiz et al. 1999; Byers 2002; Scaffelke and Hewitt 2007). Although difficult to discern, there are in general three broad categories of impacts from introduced marine species: ecosystem impacts, economic impacts, and human health impacts.

4.1 ECOSYSTEM IMPACTS

Parker et al. (1999) developed a model where the impacts of introduced species are measured at multiple levels: effects on individuals, genetic effects, population dynamic effects (community effects), and effects on ecosystem processes. These impacts can work separately or in combination for any species or suite of species and can range from small localized impacts to larger-scale regional impacts. Table 3 describes examples of impacts of introduced species on native species in the Gulf of Maine.

One of the most well studied impacts in the Gulf of Maine is community shifts resulting from the cumulative effect of two marine invaders—the bryozoan *Membranipora membranacea* and the green alga *Codium fragile* ssp. *fragile*—on native laminarian kelps. Kelp beds in the Gulf of Maine provide critical habitat for a wide range of species, such as native fish and invertebrates (Steneck et al. 2002). Historically, grazing by sea urchins was the major source of disturbance in kelp beds, leading to bare patches and, at times, large-scale removal (urchin barrens) (Johnson and Mann 1998). In the past, kelp would generally re-establish after most disturbances. However, in the late 1980s, a dramatic transformation of kelp beds began in the Gulf of Maine concurrent with the arrival of *M. membranacea*.

Membranipora membranacea, a native of Europe, was first recorded in the Gulf of Maine in 1987, and within three years became the dominant kelp epiphyte in

FLEETING IMPACTS?

Allmon and Sebens (1988) describe the rise and fall of one invader in the Gulf of Maine, the sea slug *Tritonia plebeia*. It was first observed in 1983 on subtidal rock walls in Nahant, Massachusetts, and in just two years its density exceeded that of all other nudibranchs at the site. Predation by *T. plebeia* on the native soft coral *Alcyonium siderium* led to bare patches in the dense coral canopy, which allowed sea urchins to access and prey upon the exposed coral fronds. The combination of predation by *T. plebeia* and sea urchins led to large declines and even complete displacement of *A. siderium* at some locations. While the invasion of *T. plebeia* resulted in significant and cascading impacts on the soft coral community in Nahant, its occurrence was short lived. *Tritonia plebeia* has been rare or absent in Nahant since 1986. It is uncertain whether the slug has returned elsewhere and what influenced its rapid increase and decline.

Table 3: Examples of marine invasive species impacts on native species in the Gulf of Maine.

NATIVE SPECIES	IMPACT	SOURCE
Mytilus edulis (blue mussel)*	• *Hemigrapsus sanguineus* feeds on juveniles, consumes up to 150 mussels per crab per day in the laboratory, comprises 30% of the diet in the field • Flatworm *Convoluta convoluta* feeds on juveniles • Makes up to 45% of the diet of *Carcinus maenas*	Loher and Whitlatch 2002; Byrnes and Witman 2003; Griffen and Delaney 2007
Mya arenaria (soft shell clam)*	• In caging experiments, *C. maenas* removed 80% of small *M. arenaria* and consumed up to 22 clams per crab per day	Floyd and Williams 2004
Homarus americanus (lobster)*	• *C. maenas* arrives to food faster and defends food resources from juvenile lobsters in the laboratory	Williams et al. 2006
Littorina saxatilis (periwinkle)	• Growth rate is reduced when competing with *Littorina littorea* • Susceptible to predation by *C. maenas*	Eastwood et al. 2007
Ilyanassa obsoleta (mud snail)	• *L. littorea* competitively displaces *I. obsoleta* from habitat • *C. maenas* and *L. littorea* feed on egg capsules	Brenchley 1982; Brenchley and Carlton 1983
Fucus spp. (rockweed)	• *L. littorea* can prevent establishment of *Fucus* on smooth surfaces by grazing small germlings	Lubchenco 1983

* Important commercially in the Gulf of Maine

offshore locations of New Hampshire and Maine (Berman et al. 1992; Lambert et al. 1992; Schwaninger 1999). Kelp blades encrusted with *M. membranacea* are more susceptible to breakage and are also heavily consumed by sea urchins and the native gastropod *Lacuna vincta* (Lambert et al. 1992; Levin et al. 2002). Increased drag and heavy grazing pressure on blades encrusted with *M. membranacea* leads to extensive kelp defoliation during winter storm events (Lambert et al. 1992, Levin et al. 2002). The resulting large, bare patches within the kelp bed provide space for another invader, the green alga *Codium fragile* ssp. *fragile* to establish (Levin et al. 2002).


Photo: MIT Sea Grant

Codium fragile ssp. *fragile* (previously known as *Codium fragile* ssp. *tomentosoides*) was introduced to the Gulf of Maine as a hitchhiker on oysters transplanted from Long Island Sound and also may have drifted through the Cape Cod Canal from southeast Massachusetts (Wood 1962; Carlton and Scanlon 1985; Mathieson et al. 2003). This species (further referred to as *C. fragile*) cannot directly displace standing kelp but opportunistically colonizes areas after disturbance (Levin et al. 2002). The pattern of defoliation of kelp blades encrusted with *M. membranacea* and subsequent colonization of the former kelp bed by *C. fragile* has occurred to such an extent in the Gulf of Maine that it is now the dominant canopy species in some locations (Harris and Tyrell 2001; Mathieson et al. 2003). For example, at the Isle of Shoals, *C. fragile* increased 20-fold and kelp cover decreased from 44 percent to 2 percent in ten years (Levin et al. 2002). Similarly, sites in New Hampshire and Maine have experienced 27-fold increases of *C. fragile* over a 22-year period (Mathieson et al. 2008c).

It is unclear how the transformation of kelp beds to *C. fragile* meadows impacts ecosystems of the Gulf of Maine. *Codium fragile* ssp. *fragile* and kelp morphologies are not similar, and establishment of *C. fragile* in former kelp beds may modify the habitat to such an extent that there are wholesale shifts in the species assemblage (Schmidt and Scheibling 2007). For example, the native wrasse *Tautogolabrus adspersus* (cunner) recruits six times higher in kelp than in *C. fragile* meadows (Levin et al. 2002). The rise in *C. fragile* has also led to an increase in its associated epiphyte, *Neosiphonia harveyi*, whose population has increased six-fold since 1966 (Mathieson et al. 2003). *Neosiphonia harveyi* is now one of the most widely distributed algal species in the Gulf of Maine (Mathieson et al. 2008c).

4.2 ECONOMIC IMPACTS

There are few empirical studies focused on the economic impacts of marine introduced species in the Gulf of Maine and elsewhere (Stone and Lovell 2005). In general, economic impacts of non-native species may include monetary costs for management, cost and damages incurred due to fouling of equipment and vessels, aesthetic and/or recreation impacts, and actual losses relative to impacts to fishery or aquaculture resources. In the Gulf of Maine, fouling, particularly by invasive tunicates, and impacts to commercially harvested species is a concern (see Table 3). Fouling by tunicates on gear and harvested product is a major issue for the mussel farming industry in Canada, where approximately 2-3 tonnes of bivalves are harvested each year in New Brunswick and Nova Scotia (Locke et al. 2007). Predation by *Carcinus maenas* on *Mya arenia* (soft shell clam) is implicated in the decline of harvest and value (Glude 1955). Total costs associated with the *C. maenas* invasion in the US are estimated at $44 million, but it is unclear how this figure was derived (Pimentel et al. 2005). In addition, non-native marine species may result in aesthetic impacts that alter recreation and are costly to clean up. For example, *C. fragile* often washes ashore and forms large clumps on beaches that are unsightly and result in noxious odors (Pederson et al. 2005).

4.3 PUBLIC HEALTH IMPACTS

Impacts to public health are included in the suite of potential impacts of marine invaders, although not much is known regarding public health impacts in the Gulf of Maine specifically. Introduced pathogens, such as *Vibrio cholera*, the bacteria responsible for cholera in humans, have been found in ballast water and could potentially be discharged to local waters (Ruiz et al. 2000b). Organisms that result in concentrated toxins in seawater and/or seafood are also a concern. For example, the non-native dinoflagellate *Alexandrium minutum* may contribute to red tide outbreaks south of the Gulf of Maine (Carlton 2003). The majority of pathogenic and/or toxic organisms are microscopic and require specific, and at times, cost-intensive monitoring techniques. There is likely a wide array of potential invasive pathogens that are currently overlooked in the Gulf of Maine due to a lack of targeted monitoring programs (Carlton 2003).

5. Actions and Responses

Focused efforts on the management of marine invasive species are a relatively recent phenomenon. In contrast with terrestrial invasions, government and other agents have been slow to recognize marine introductions as an issue, primarily due to a lack of information and demonstrable impacts to human health, ecosystems, and economies (Hewitt et al. 2009; Ruiz et al. 1999; Stone and Lovell 2005; Scaffelke and Hewitt 2007). Responses exist on several scales; there are numerous international and national efforts relative to invasive species (see Table 4 for a summary) in addition to regional and local initiatives. While some efforts include a regulatory component, the bulk of management approaches to marine invasive species are voluntary.

5.1 NATIONAL

In the Gulf of Maine, the primary instrument for prevention of marine introductions is the regulation of ballast water by the US Coast Guard under the National Invasive Species Act and Transport Canada under the Canada Shipping Act. Mandatory ballast water exchange and reporting requirements have been in place for all US waters since 2004 and in Canada since 2000 (Transport Canada 2010). There has been a recent push by the US Coast Guard to implement ballast water discharge standards similar to those recently proposed by the International Maritime Organization (IMO 2004; USCG 2009). The process includes a phased approach of performance standards based upon number of living organisms, to be reached primarily through ballast water treatment technologies and an eventual phase out of ballast water exchange (USCG 2009). In addition, a recent US Supreme Court decision has led the US Environmental Protection Agency (US EPA) to regulate discharges incidental to the normal operation of vessels, including aquatic invasive species (AIS) in ballast water and biofouling, as a pollutant under the National Pollutant Discharge Elimination System (NPDES) (US EPA 2009). Lodge et al. (2006) make several recommendations to improve introduced species management in the United States, including: better management of invasive species pathways, adoption of more quantitative risk assessment procedures, use of cost-effective diagnostic and surveillance activities to improve communication, creation of new legal authorities and emergency funding for rapid response, increased funding to slow the spread of invaders and protect habitats and infrastructure, and the establishment of a national center for invasive species management.

5.2 REGIONAL AND TRANSBOUNDARY

No official transboundary regulatory effort exists between the governments of the United States and Canada for the Gulf of Maine specifically. The Northeast Aquatic Nuisance Species Panel serves as the major coordinating body for the

Table 4: Examples of international and national responses to marine introduced species.

INTERNATIONAL	
United Nations	• Environmental Program, Agenda 21, Chapter 17 (1992): addresses the issue of aquatic invasives in the context of ballast water and aquaculture • Food and Agriculture, Code of Conduct for Responsible Fisheries (1995): covers fishing practices and aquaculture • Convention on Biological Diversity, Article 8(h) (1993): commitment to prevent the introduction, and to control and eradicate alien species • International Maritime Organization (2004): International Convention for the Control and Management of Ships' Ballast Water and Sediments (2004)
International Council for Exploration of the Seas (ICES)	• Code and Practice on the Introduction and Transfer of Marine Organisms (2004): aquaculture focused
NATIONAL	
United States	• Lacey Act (1990): limited to controlling intentional introductions of injurious species • Nonindigenous Aquatic Nuisance Species Prevention and Control Act (NANPCA) (1990): regulate ballast water in the Great Lakes and establishment of the Aquatic Nuisance Species (ANS) Task Force • ANS Task Force (1990): coordinates federal activities, provides funding and direction to regional panels, directs states to develop management plans, provides limited funding for plan implementation • National Invasive Species Act (1996): amended NANPCA to broaden ballast water requirements to the entire US • Presidential Executive Order No. 13112 (1999): created the National Invasive Species Council • National Invasive Species Council, National Invasive Species Management Plan (2001): serves as national blueprint for invasive species management
Canada	• Canada Shipping Act, Section 657.1 (2001): provides for the power to pass ballast water regulations • An Invasive Alien Species Strategy for Canada (2004): national strategy for invasive species management • The Invasive Alien Species Partnership Program (2004): provides funding in support of the goals of the Invasive Alien Species Strategy • Canadian Biodiversity Strategy (1995): provides means to anticipate, identify and monitor alien organisms, screening standards, and risk assessment • National Wildlife Policy (1990): nonindigenous species should not be introduced into natural systems • Canadian Environmental Protection Act (1999): applies an ecological risk assessment process before permitting the introduction of any new species • Fisheries Act (1985): develops a standard ecological risk assessment process, specifically in the context of fish stocking, live bait, and aquaculture • National Code on Introductions and Transfers of Aquatic Organisms (2003): assesses proposals for moving aquatic organisms between water bodies

Sources: Doelle 2001; Canada Shipping Act 2001; Government of Canada 2004; IMO 2004; Hewitt et al. 2009.

Northeast region, and all Gulf of Maine states and provinces have delegates that sit on the panel. In Atlantic Canada, the Canadian Council of Fisheries and Aquaculture Ministers, Aquatic Invasive Species Task Group is responsible for the development of an action plan to address the threat of aquatic invasive species, and the Council of Atlantic Premiers recently signed a Memorandum of Understanding (MOU) for the Development of the Aquaculture Sector that also addresses invasive species (CCFAM 2004; COAP 2008). The Marine Monitoring and Information Collaborative, coordinated out of the Massachusetts Office of Coastal Zone Management (MA CZM), is a volunteer early detection and monitoring network for marine invasive species that includes numerous sites in Maine, New Hampshire, and Massachusetts (MA CZM 2008). The Rapid Assessment Survey, a partnership between the Massachusetts Institute of Technology Sea Grant Program, MA CZM, and National Estuary Programs in New England, is conducted by a team of expert taxonomists who examine marine fouling communities in New England and Long Island Sound (Pederson et al. 2005). The surveys have been conducted roughly every three years since 2000, with the next survey planned for summer 2010.

5.3 STATE AND PROVINCIAL

Provincial and state management of marine invasive species is largely vector based, with aquaculture as a prime example. States and provinces largely have permitting jurisdiction over operation of aquaculture facilities, including the transfer and source of aquaculture species, and other projects in the marine realm that could potentially introduce or spread marine invasive species. For example, in New Brunswick a permit can be refused if the regulator determines that the proposed operation poses an unacceptable risk to the environment, however the threat of invasive species is not specifically identified (Doelle 2001). Most state and provinces within the Gulf of Maine do not have programs dedicated to marine invasive species management; rather management often falls under a variety of environmental agencies and programs (Doelle 2001). For example, while Massachusetts has an Aquatic Invasive Species Program, a Management Plan, and an Aquatic Invasive Species Group, these do not hold any regulatory authority. In addition, there are at least six other entities that are involved with aquatic invasive species management to some degree (MA CZM 2002). A tool that states and provinces can use for marine invasive species management is to add on to pending federal regulation in the form of comments or conditions. For example, Maine and Massachusetts added conditions to the recent US EPA Vessel General Permit limiting underwater husbandry, and Massachusetts also included provisions requiring ballast water exchange for ships engaged in coastwide trade (US EPA 2009).

INDICATOR SUMMARY

INDICATOR	POLICY ISSUE	DPSIR	TREND*	ASSESSMENT
Number of established marine invasive species	Growth in global trade and other human activities	Driving Force, Pressure	–	Fair
Distribution and spread of marine invasives	Increase in regional vectors and habitat pressures (i.e., hull fouling, aquaculture, habitat modification, climate change)	Pressure	–	Poor
Losses incurred by fishery and aquaculture industry	Losses of fishery resources from invasive species impacts	Impacts	/	Fair
Costs incurred or spent on invasive species management	Investment in marine invasive management programs and education	Responses	/	Poor

* KEY:
– Negative trend
/ Unclear or neutral trend
+ Positive trend
? No assessment due to lack of data

Data Confidence

- Information on number of species in the Gulf of Maine was derived through literature review and confirmed reports of species, and this may not reflect the actual number of marine invasives.
- Native status has not been determined for all taxa, and cryptogenic species were not included in this review, thus species may be underestimated.

Data Gaps

- Caution must be taken with marine invasive species estimates in the Gulf of Maine since large data gaps exist.
- There is a lack of information on impacts, particularly economic impacts, of marine invasive species in the Gulf of Maine. There is a general sense that impacts are occurring in the fisheries and aquaculture industries, but it is unclear whether this results in significant losses.
- The majority of information on marine invasive species is from coastal and estuarine systems.
- Not all habitats or taxa are adequately addressed in monitoring programs.
- There is a lack of empirical studies on the impacts of marine invasive species in the Gulf of Maine and elsewhere.

6. References

Aieta AE and Oliveira K. 2009. Distribution, prevalence, and intensity of the swim bladder parasite *Anguillicola crassus* in New England and eastern Canada. Diseases of Aquatic Organisms 84: 229-235.

Allmon RA and Sebens KP. 1988. Feeding biology and ecological impact of an introduced nudibranch, *Tritonia plebia*, New England, USA. Marine Biology 99: 375-385.

Barry JP, Baxter CH, Sagarin RD and Gilman SE. 1995. Climate-related, long-term faunal changes in a California rocky intertidal community. Science 267(5198): 672-675.

Beckman C and Menzies R. 1960. The relationship of reproductive temperature and the geographical range of the marine woodborer *Limnoria tripunctata*. Biological Bulletin 118(1):9-16.

Bégin C and Scheibling RE. 2003. Growth and survival of the invasive green alga *Codium fragile* ssp. *tomentosoides* in tide pools on a rocky shore in Nova Scotia. Botanica Marina 46(5): 404-412.

Berman J, Harris L, Lambert W, Buttrick M and Dufrensne M. 1992. Recent invasions of the Gulf of Maine: Three case histories. Conservation Biology 6: 435-441.

Blezard DJ. 1999. Salinity as a refuge from predation in a nudibranch-hydroid relationship within the Great Bay Estuary system [thesis]. Durhams (NH): University of New Hampshire. 77p.

Bouchard DA, Brockway K, Giray C, Keleher W and Merrill PL. 2001. First report of infectious salmon anaemia (ISA) in the United States. European Association of Fish Pathologists Bulletin 21(2): 86-88.

Bower SM. 2007. Synopsis of Infectious Diseases and Parasites of Commercially Exploited Shellfish: *Haplosporidium nelsoni* (MSX) of Oysters. http://www.pac.dfo-mpo.gc.ca/science/species-especes/shellfish-coquillages/diseases-maladies/pages/hapneloy-eng.htm (accessed March 2010).

Brawley SH, Coyer J, Blakesee AMH, Hoarau G, Johnson LE, Byers JE, Stam WT and Olsen JL. 2009. Historical invasions of the intertidal zone of Atlantic North America associated with distinctive patterns of trade and emigration. Proceedings of the National Academy of Science 106(20): 8239-8244.

Brenchley GA. 1982. Predation on encapsulated larvae by adults: effects of introduced species on the gastropod *Ilyanassa obsoleta*. Marine Ecology Progress Series 9:255-262.

Brenchley GA and Carlton JT. 1983. Competitive displacement of native mud snails by introduced periwinkles in the New England intertidal zone. Biological Bulletin 165: 543-558.

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 and 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.

Byers JE. 2002. Impact of non-indigenous species enhanced by anthropogenic alteration of selection regimes. Oikos 97(3): 449-458

Byrnes J and 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.

Canada. 2004. An invasive alien species strategy for Canada. 46 p. http://www.ec.gc.ca/eee-ias/98DB3ACF-94FE-4573-AE0F-95133A03C5E9/Final_IAS_Strategic_Plan_smaller_e.pdf (accessed March 2010).

Canada Shipping Act. 2001. Ballast Water Control and Management Regulations SOR/2006-129.

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

Carlton JT. 1992. Introduced marine and estuarine mollusks of North America: An end-of–the-20th-century perspective. Journal of Shellfish Research 11(2): 489-505.

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

Carlton JT. 1996b. Marine bioinvasions: The alteration of marine ecosystems by nonindigenous species. Oceanography. 9(1): 36-43.

Carlton JT. 2003. A checklist of the introduced and cryptogenic marine and estuarine organisms from Nova Scotia to Long Island Sound. 2nd Edition. Williams College–Mystic Seaport Maritime Studies Program. Mystic, CT.

Carlton JT. 2004. A preliminary checklist of the introduced marine and estuarine organisms on the coast of Maine, U.S.A. Williams College–Mystic Seaport Maritime Studies Program. Mystic, CT.

Carlton JT and Geller JB. 1993. Ecological roulette: The global transport and invasion of nonindigenous marine organisms. Science 261: 78-82.

Carlton JT and Hodder J. 1995. Biogeography of coastal marine organisms: Experimental studies on a replica of a sixteenth century sailing vessel. Marine Biology 121: 721-730.

Carlton JT and Scanlon JA. 1985. Progression and dispersal of an introduced alga: *Codium fragile* ssp *tomentosoides* (Chlorophyta) on the Atlantic coast of North America. Botanica Marina 28: 155-165.

Cohen AN and Carlton JT. 1998. Accelerating invasion rate in a highly invaded estuary. Science 279(5350): 555-558.

Cone DK and Marcogliese DJ .1995 *Pseudodactylogyrus anguillae* on *Anguilla rostrata* in Nova Scotia: An endemic or an

introduction? Journal of Fish Biology 47(1): 177–178.
Cook T, Folli M, Klinck J, Ford S and Miller J. 1998. The relationship between increasing sea-surface temperature and the northward spread of *Perkinsus marinus* (Dermo) disease epizootics in oysters. Estuarine, Coastal and Shelf Science 46: 587-597.
Coutts ADM and 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.
Delaney DG, Sperling CD, Adams CS and Leung B. 2008. Marine invasive species: Validation of citizen science and implications for national monitoring networks. Biological Invasions 10(1): 117-128.
Dijkstra J, Harris LG and 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 and 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.
Doelle M. 2001. Legal and policy responses to invasive species, background paper. Prepared for the Commission for Environmental Cooperation. 40 pp.
Drake JM and Lodge DM. 2007. Hull fouling is a risk factor for intercontinental species exchange in aquatic ecosystems. Aquatic Invasions 2(2): 121-131.
Eastwood MM, Donahue MJ and Fowler AE. 2007. Reconstructing past biological invasions: Niche shifts in response to invasive predators and competitors. Biological Invasions 9(4): 397-407.
Elton CS. 1958. The Ecology of Invasions by Animals and Plants. London: Chapman and Hall. 226 pp.
Farnham WF. 1980. Studies on aliens in the marine flora of southern England. In: Price JH, Irvine DEG, Farnham WF (Editors). The Shore Environment, Volume 2: Ecosystems. London: Academic Press. pp. 875-914.
Floyd T and Williams J. 2004. Impact of green crab (*Carcinus maenas* L.) predation on a population of soft-shell clams (*Mya arenaria* L.) in the southern Gulf of St. Lawrence. Journal of Shellfish Research 23(2): 457-462.
Ford SE. 1996. Range expansion of the oyster parasite *Perkinsus marinus* into the northeastern United States: Response to climate change? Journal of Shellfish Research 15(1): 45-56.
Gavio B and Fredericq S. 2002. *Grateloupia turuturu* (Halymeniaceae, Rhodophyta) is the correct name of the non-native species in the Atlantic known as *Grateloupia doryphora*. European Journal of Phycology 37:349-359.
Glasby TM, Connell SD, Holloway MG and Hewitt CL. 2007. Nonindigenous biota on artificial structures: Could habitat creation facilitate biological invasions? Marine Biology 151(3): 887-895.
Glude JB. 1955. The effect of temperature and predators on the abundance of the soft-shell clam, *Mya arenia*, in New England. Transactions of the American Fisheries Society 84(1): 13-26.
Government of Canada. 2004. An invasive alien species strategy for Canada. http://www.ec.gc.ca/eee-ias (accessed May 2010). 46 p.
Griffen BD and Delaney DG. 2007. Species invasion shifts the importance of predator dependence. Ecology 88(12): 3012-3021.
Hare JA and Whitfield PE. 2003. An integrated assessment of the introduction of lionfish (*Pterois volitans/miles* complex) to the Western Atlantic Ocean. NOAA Technical Memorandum NOS NCCOS 2. 31 pp.
Harlin MM and Villalard-Bohnsack M. 2001. Seasonal dynamics and recruitment strategies of the invasive seaweed *Grateloupia doryphora* (Halymeniaceae, Rhodophyta) in Narragansett Bay and Rhode Island Sound, Rhode Island, USA. Phycologia 40(5): 468-474.
Harris LG and Dijkstra JA. 2007. Seasonal appearance and monitoring of invasive species in the Great Bay estuarine system: A final report to the New Hampshire Estuaries Project. 27 pp.
Harris LG and Tyrell MC. 2001. Changing community states in the Gulf of Maine: Synergism between invaders, overfishing and climate change. Biological Invasions 3: 9-21.
Hayward CJ, Iwashita M, Crane JS and Ogawa K. 2001. First report of the invasive eel pest *Pseudodactylogyrus bini* in North America and in wild American eels. Diseases of Aquatic Organisms 44:53-60.
Hellmann JA, Byers JS, Bierwagen BG and Dukes JS. 2008. Five potential consequences of climate change for invasive species. Conservation Biology 22(3): 534-543.
Hewitt CL, Everett RA and Parker N. 2009. Examples of current international, regional, and national regulatory frameworks for preventing and managing marine bioinvasions. In: Rilov G, Crooks JA (Editors). Biological Invasions in Marine Ecosystems Ecological, Management, and Geographic Perspectives. Berlin, Heidelberg: Springer-Verlag. pp. 335-349.
Hines AH, Miller AW, Ruiz GM and Lion K. 2004. Estimating Domestic and Foreign Ballast Water as a Vector for Invasive Species: Regional Analysis for New England, Northeast North America. In: Pederson, J (Editor). Ballast Water Exchange: Exploring the Feasibility of Alternate Ballast Water Exchange Zones in the North Atlantic. Cambridge: Massachusetts Institute of Technology. pp. 53-63.
Hooper R and South GR. 1977. Additions to the benthic marine algal flora of Newfoundland III, with observations on species new to eastern Canada and North America. Naturaliste canada 104:383-394.
International Maritime Organization (IMO). 2004. International Convention for the Control and Management of Ships' Ballast Water and Sediments. http://www.imo.org/Conventions/Mainframe.asp?topic_id=867 (accessed March 2010).
National Invasive Species Council, Invasive Species Advisory Committee (ISAC). 2006. Invasive Species Definition Clarification

and Guidance White Paper. 11p. http://www.invasivespecies.gov/global/ISAC/ISAC_index.html (accessed March 2010).
Johnson GM and Mann KH. 1998. Diversity, patterns of adaptation, and stability of Nova Scotian kelp beds. Ecological Monographs 58: 129-154.
Lambert WJ, Levin PS and Berman J. 1992. Changes in the structure of a New England (USA) kelp bed: The effects of an introduced species? Marine Ecology Progress Series 88: 303-307.
Larsen PF and Doggett LF. 1991. The macroinvertebrate fauna associated with the mud flats of the Gulf of Maine. Journal of Coastal Research 7(2): 365-375.
Levin PS, Coyer JA, Petrik R and Good T. 2002. Community-wide effects of nonindigenous species on temperate rocky reefs. Ecology 83(11): 3182-3193.
Locke A, Hanson JM, Ellis KM, Thompson J and Rochette R. 2007. Invasion of the southern Gulf of St. Lawrence by the clubbed tunicate (*Styela clava* Herdman): Potential mechanisms for invasions of Prince Edward Island Estuaries. Journal of Experimental Marine Biology and Ecology 342: 69-77.
Lodge DM, Williams S, MacIsaac HJ, Hayes KR, Leung B, Reichard S, Mack RN, Moyle PB, Smith M, Andow DA, Cartlon JT and McMichael A. 2006. Biological invasions: Recommendations for U.S. policy and management. Ecological Applications 16(6): 2035-2054.
Loher AM and Whitlatch RB. 2002. Relative impacts of two exotic brachyuran species on blue mussel populations in Long Island Sound. Marine Ecology Progress Series 227: 135-144.
Lubchenco J. 1983. *Littorina* and *Fucus*: Effects of herbivores, substratum heterogeneity, and plant escapes during succession. Ecology 64(5): 1116-1123.
Martine JL and LeGresley MM. 2008. New phytoplankton species in the Bay of Fundy since 1995. ICES Journal of Marine Science 65: 759-764.
Massachusetts Office of Coastal Zone Management (MA CZM). 2002. Massachusetts Aquatic Invasive Species Management Plan, Massachusetts Aquatic Invasive Species Working Group. 56 pp. http://www.mass.gov/czm/invasives/background/plan.htm (Accessed April 2010)
Massachusetts Office of Coastal Zone Management (MA CZM). 2008. Monitoring Marine Invasive Species: Guidance and Protocols for Volunteer Monitoring Groups. 44 p. http://www.mass.gov/czm/invasives/docs/mimic_guide_web.pdf (accessed April 2010).
Mathieson AC, Dawes CJ, Harris LG and Hehre EJ. 2003. Expansion of the Asiatic green alga *Codium fragile* subsp. *tomentosoides* in the Gulf of Maine. Rhodora 105: 1-53.
Mathieson AC, Hehre EJ, Dawes CJ and Neefus CD. 2008a. A historical comparison of seaweed populations from Casco Bay Maine. Rhodora 110(941): 1-102.
Mathieson AC, Pederson J and Dawes CJ. 2008b. Rapid assessment surveys of fouling and introduced seaweeds in the northeastern Atlantic. Rhodora 110(944): 406-478.
Mathieson AC, Pederson JR, Neefus CD, Dawes CJ and Bray TL. 2008c. Multiple assessments of introduced seaweeds in the North Atlantic. ICES Journal of Marine Science 65: 730–741.
Mathieson A, Dawes C, Pederson J, Gladych R and Carlton J. 2008d. The Asian red seaweed *Grateloupia turuturu* (Rhodophyta) invades the Gulf of Maine. Biological Invasions 10(7): 985-988.
Maurer D and Wigley RL. 1982. Distribution and ecology of mystids in Cape Cod Bay, Massachusetts. Biological Bulletin 163: 477-491.
McDermott JJ. 1991. A breeding population of the Western Pacific crab *Hemigrapsus sanguineus* (Crustacea: Decapoda: Grapsidae) established on the Atlantic coast of North America. Biological Bulletin 181: 195-198.
McKindsey CW, Landry T, O'Beirn FX and Davies I. 2007. Bivalve aquaculture and exotic species: A review of ecological considerations and management issues. Journal of Shellfish Research 26(2): 281-294.
McIvor LM and Stanhope MJ. 2000. Systematics and phylogeography of the invasive red alga, *Polysiphonia harveyi*. Journal of Phycology 36(3): 46-47.
Osman RW and Whitlatch RB. 2007. Variation in the ability of *Didemnum* sp. to invade established communities. Journal of Experimental Marine Biology and Ecology 342: 40-53.
Pappal AL. 2006. Cobble habitat preferences of juvenile winter flounder, *Pleuronectes americanus*, and comparison of laboratory observation techniques [thesis]. Dartmouth (MA): University of Massachusetts. 95 pp.
Parker IM, Simberloff D, Lonsdale WM, Goodell K, Wonham M, Kareiva PM, Williamson MH, Van Holle B, Moyle PB, Byers JE and Goldwasser L. 1999. Impact: Toward a framework for understanding the ecological effects of invaders. Biological Invasions 1: 3-1.
Pederson J, Bullock R, Carlton JT, Dijkstra J, Dobroski N, Dyrynda P, Fishers R, Harris L, Hobbs N, Lambert G, Lazo-Wasem E, Mathieson A, Miglietta M, Smith J, Smith J III and Tyrrell M. 2005. Marine invaders in the northeast: Rapid assessment survey of non-native and native marine species of floating dock communities, report of the August 3-9, 2003, survey. Publication No. 05-03. Cambridge: Massachusetts Institute of Technology, Sea Grant College Program. 40 pp.
Pimentel D, Zuniga R and Morrison D. 2005. Update on the environmental and economic costs associated with alien-invasive species in the United States. Environmental Economics 52: 273-288.
Rivest BR, Coyer J and Tyler S. 1999. The first known invasion of a free-living marine flatworm. Biological Invasions 1: 393-394.

Rudnick D, Veldhuizen T, Tullis R, Culver C, Hieb K and Tsukimura B. 2005. A life history model for the San Francisco Estuary population of the Chinese mitten crab, *Eriochier sinensis* (Decapoda: Grapsoidea). Biological Invasions 7: 333-350.

Ruiz GM, Fofonoff P, Hines AH and Grosholz ED. 1999. Non-indigenous species as stressors in estuarine and marine communities: Assessing invasion impacts and interactions. Limnology and Oceanography 44(3): 950-972.

Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ and Hines AH. 2000a. Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. Annual Review of Ecology and Systematics 31: 481-531.

Ruiz GM, Rawlings TK, Dobbs FC, Drake LA, Mullady T, Huq A and Colwell RR. 2000b. Global spread of microorganisms by ships. Nature 408: 49-50.

Ruiz GM, Fegley L, Fofonoff P, Cheng Y and Lemaitre R. 2006. First records of *Eriocheir sinensis* H Milne Edwards, 1853 (Crustacea: Brachyura: Varunidae) for Chesapeake Bay and the mid-Atlantic coast of North America. Aquatic Invasions 1(3): 137-142.

Scaffelke B and Hewitt CL. 2007. Impacts of introduced seaweeds. Botanica Marina 50:397-417.

Scheibling RE, Hennigar AW and Balch T. 1999. Destructive grazing, epiphytism, and disease: The dynamics of sea urchin–kelp interactions in Nova Scotia. Canadian Journal of Fisheries and Aquatic Sciences 56: 2300–2314

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

Schwaninger HR. 1999. Population structure of the widely dispersing marine bryozoan *Membranipora membranacea* (Cheilostomata): Implications for population history, biogeography, and taxonomy. Marine Biology 135: 411–423.

Smith RT. 1964. Keys to Marine Invertebrates of the Woods Hole Region: A Manual for the Identification of the More Common Marine Invertebrates. Woods Hole (MA): Woods Hole Oceanographic Institution, Marine Biological Laboratory.

Stachowicz JJ, Terwin JR, Whitlatch RB and Osman RW. 2002. 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(24): 15497-15500.

Steneck RS, Graham MH, Bourque BJ, Corbett D, Erlandson JM, Estes JA and Tegner MJ. 2002. Kelp forest ecosystems: Biodiversity, stability, resilience and future. Environmental Conservation 29(4): 436-459.

Stone SF and Lovell S. 2005. The economic impacts of aquatic invasive species: A review of the literature. United States Environmental Protection Agency, National Center for Environmental Economics. Working Paper #05-02. 66 pp.

Swan EF. 1956. Isopods of the genus *Ligia* on the New England coast. Ecology 37(1): 204-206.

Transport Canada. 2010. A Guide to Canada's Ballast Water Control and Management Regulations TP 13617 E. http://www.tc.gc.ca/eng/marinesafety/tp-tp13617-menu-2138.htm (accessed March 2010).

Trott TJ. 2004. Cobscook Bay Inventory: A historical checklist of marine invertebrates spanning 162 years. Northeastern Naturalist 11(2): 261-324.

Tyrrell MC and Byers JE. 2007. Do artificial substrates favor nonindigenous fouling species over native species? Journal of Experimental Marine Biology and Ecology 342: 54-60.

United States Coast Guard (USCG). 2009. Standards for living organisms in ship's ballast water discharged in U.S. waters. Federal Register 74(166): 44631-44672.

United States Environmental Protection Agency (US EPA). 2009. Vessel general permit for discharges incidental to the normal operation of vessels. 165 p. http://www.epa.gov/npdes/pubs/vessel_vgp_permit.pdf (accessed March 2010).

Valentine PC, Collie JS, Reid RN, Asch RG, Guida VG and Blackwood, D. 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.

Valentine PC, Carman MR, Dijkstra J and Blackwood DS. 2009. Larval recruitment of the invasive colonial ascidian *Didemnum vexillum*, seasonal water temperatures of New England coastal and offshore waters, and implications for spread of the species. Aquatic Invasions 4(1): 153-168.

Veilleux É and de Lafontaine Y. 2007. Biological synopsis of the Chinese mitten crab (*Eriocheir sinensis*). Canadian Manuscript Report of Fisheries and Aquatic Sciences 2812. 53 pp.

Wasson K, Von Holle B, Toft J and Ruiz G. 2000. Detecting invasions of marine organisms: Kamptozoan case histories. Biological Invasions 2(1): 59-74.

Wethey DS. 2002. Biogeography, competition, and microclimate: The barnacle *Chthamalus fragilis* in New England. Integrative and Comparative Biology 42(2): 872-880.

Whitfield PE, Gardner T, Vives SP, Gilligan MR, Courtenay WR, Ray C and Hare J. 2002. Biological invasion of the Indo-Pacific lionfish *Pterois volitans* along the Atlantic coast of North America. Marine Ecology Progress Series 235: 289-297.

Whitfield PE, Hare JA, David AW, Harter SL, Munoz RC and Addison CM. 2007. Abundance estimates of the Indo-Pacific lionfish *Pterois volitans/miles* complex in the Western North Atlantic. Biological Invasions 9(1): 53-64.

Williams PJ, Floyd TA and Rossong MA. 2006. Agonistic interactions between invasive green crabs, *Carcinus maenas* (Linnaeus), and sub-adult American lobsters, *Homarus americanus* (Milne Edwards). 2006. Journal of Experimental Marine Biology and Ecology 329: 66-74.

Wood RD. 1962. *Codium* is carried to Cape Cod. Bulletin of the Torrey Botanical Club 89(3): 178-180.