UNDERWATER ALIENS: QUANTIFYING PROPAGULE PRESSURE OF AQUATIC INVASIVE SPECIES IN CANADIAN SHIPPING PORTS

by

VERONICA BETHANY PUI GWUN LO

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ABSTRACT

Increased trading worldwide has created introduction pathways for aquatic invasive species (AIS), particularly through shipping activities. In our research, we used ballast discharge data and estimates of the wetted surface area of vessels to provide preliminary estimates of the potential propagule pressure ballast and hull fouling organisms on Canadian shipping ports from the commercial shipping sector. We compared total wetted surface area, vessel arrivals and ballast discharge across shipping ports and vessel categories in the Atlantic, Great Lakes-St. Lawrence and Pacific shipping regions. Using these potential propagule pressure estimates for ballast organisms, we developed a model, building on that of MacIsaac et al.'s (2002), to characterize the effective propagule pressure of aquatic non-native species to Canadian shipping ports. Our model includes the effects of environmental similarity between destination and source on mortality, which can be considerable. We parameterized the model using recent nationally and regionally collected databases on ship voyages, and abundance surveys yielding mortality rates of several zooplankton species. These empirically derived parameters were used in our model to predict abundances of live individuals after ballast is discharged, with estimates of uncertainty and sensitivity to key assumptions. Our results indicate that for our three shipping regions, aggregate wetted surface area, vessel arrivals, and total ballast discharge were significantly correlated across shipping ports (Spearman's *ρ* ranged from 0.57 to 0.87, $p<0.05$). Correlations between these measures of propagule pressure were more variable and of varying levels of significance across vessel categories (Spearman's *ρ* ranged from 0.43 to 0.98). Our modeling results demonstrate that variation in mortality rates across tanks and voyages resulted in high variation in total effective propagule pressure. The variation between tanks and voyages has important implications for the use of mid-ocean exchange as a ballast management method for different ports and species. To our knowledge, our characterization of potential and effective propagule pressure from the commercial shipping sector is the first to be conducted on a nation-wide scale. Our

propagule pressure estimates will contribute to future efforts to determine the relationship between the establishment of aquatic invasive species and the environmental similarity between source and discharge areas.

TABLE OF CONTENTS

LIST OF TABLES

LIST OF FIGURES

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DEDICATION

for my parents Barbara Wong Lo and Don DL Lo

CO-AUTHORSHIP STATEMENT

Contributions to this thesis were made by the following:

Identification and Design of the Research Program
Colin D. Levings, Kai M.A. Chan and I contributed to the identification and design of the research in Chapter Two. Kai M.A. Chan and I identified and designed the research for Chapter Three.

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I performed all of the research in this thesis, with data provided by Nathalie Simard, Derek Gray, and Transport Canada. The research was performed under the supervision of Kai M.A. Chan, Colin D. Levings and Brian Klinkenberg.

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1. INTRODUCTION

1.1. BACKGROUND

The introduction of non-native, invasive species to ecosystems is a major threat to biodiversity (Sala et al. 2000; Wilcove et al. 1998). Whether introduced intentionally (e.g. for pest control, horticulture, or aquaculture), or unintentionally (e.g. via ballast water, or transport by land or water), invasive species can cause widespread and irreversible damage to the ecosystems they are introduced to. They predate on or compete with native species for food and habitat, interrupt the flow of ecosystem services by altering controls on critical ecosystem functions, and introduce diseases (Chapin III et al. 2000; Mack et al. 2002). For these reasons, invasive species are imposing an increasingly heavy economic toll (Pimentel et al. 2004); annually, the cost to protect Great Lakes fisheries by controlling the invasive sea lamprey is $14 million per year (Jones 2007), and the cost of introduced disease organisms to human, plant and animal health in the U.S. is estimated at $41 billion (Daszak et al. 2000). Over 400 invasive species have been identified and recorded in the Canadian Wildlife Federation Invasive Species Database (CWF 2009). Examples in Canada include sea lamprey and zebra mussels, which are now permanent residents of the Great Lakes ecosystem (Mills et al. 1994), while Eurasion water milfoil, European green crab, and various tunicate species pose serious threats to Canada's west coast (Lim 2004; Ray 2005).

1.1.1. Definitions of 'non-native' and 'invasive'

A myriad of different terms have been used to describe non-native species that have become invasive, including "exotic", "alien", "nuisance", "noxious" and "pest". It is thus necessary to make the distinction between the terms "non-native" and "invasive" and identify definitions that will be useful for the purposes of this thesis. I use a definition of non-native species that is modified from Carlton (1985) and incorporates concepts from Colautti and MacIsaac (2004): *Non-native* refers to populations of a particular species that are introduced to new habitats outside of their native range, and which may subsequently develop into viable long-term populations. This definition differs from that of Elton (1958), who defined non-native species as introduced species that can proliferate, spread and persist (Elton 1958). We consider populations of non-native species *invasive* if they proliferate and reach higher abundances than have previously been observed, and subsequently disrupt ecosystems, such as by suppressing populations of native species by habitat alteration or competition (Carlton 2002).

These impacts of invasive species often result in economic losses (e.g. reduced crop production, decreased tourism), can be costly to control and difficult to eradicate, and can be a threat to human health as agents of disease or vectors of disease-causing parasites (Mack et al. 2000). For example, the Nile Perch was introduced to Lake Victoria, East Africa, and has been attributed to dramatic declines of cichlid species as well as other negative ecosystem impacts (Witte et al. 2007). The bacterium *Vibrio cholera* is suspected to have been introduced via ballast water to Peru, causing an epidemic in 1991 that resulted in the deaths of 3000 people and more than 480,000 related illnesses (Wachsmuth et al. 1993).

Non-native populations are not always invasive. Examples of introduced, non-native species that have no documented negative effects on ecosystems include many cultivated crops, such as peaches, squash, tomatoes and maize (McNeely 2001).

Conversely, species that are ecologically or economically harmful, and that effectively behave invasively, are not always non-native. Mountain pine beetle populations, native to British Columbia, were previously suppressed every year by mortality from cold winter temperatures. However, a series of mild winters that may be a result of climate change allowed survival of the beetles over winter, which, in combination with vulnerability of even-aged stands and monocultures of pine, resulted in outbreaks that devastated over seven million ha of pine forests in British Columbia between 1999 and 2005 (Aukema et al. 2006).

1.1.2. Invasion pathways

Invasions of species or populations of a species can occur naturally, for example, when biogeographic barriers are broken down (van der Velde et al. 1996). Deliberate introduction via aquaculture, horticulture, or the animal trade can also occur. Unintended invasions can also occur as a result of human activities, via transportation pathways such as aviation, rail or commercial shipping. The latter—commercial shipping—is considered one of the principle mechanisms for the transport of non-native, aquatic invasive species (AIS) (Lavoie 1999). The shipping pathway can introduce AIS through hull fouling and the uptake and discharge of ballast water and sediment. The importance of shipping activities as a vector for AIS will increase in the future, as the global shipping industry is expected to double by the year 2020 (Gallagher 2008).

1.2. AIS INTRODUCTIONS VIA BALLAST WATER

Ships take up ballast water to replace the weight of transported cargo on return voyages, as well as to replace weight lost by fuel or water consumption. Ballast is used to maintain stability during rough weather conditions, via heavy weather compartments in the cargo holds of bulk carriers and tankers (NRC 1994). This ballast water contains viable organisms that, given suitable conditions, may become invasive after they are discharged along with the ballast at a particular location. Estimates of the volume of ballast water transferred among international waters ranges from 2 to 12 billion *t* annually (Gollasch 2007; Raaymakers 2002).

The most wide-spread method of ballast treatment is mid-ocean exchange (MOE), by which ballast water is replaced with oceanic water before it is discharged to an arrival port. The premises of MOE are that coastal organisms present at the site of ballast uptake will be discharged in the open ocean, where they will perish due to the changes in environmental parameters, particularly salinity. Organisms taken up at the site of exchange are assumed to be unable to tolerate the environmental conditions at the point of discharge.

There are a number of caveats regarding the effectiveness of MOE:

- Coastal organisms can still persist in the ballast tank after MOE (Levings et al. 2004).
- There are cases in which MOE is not required – for example, if conducting MOE would compromise the ship's stability and thus the safety of the crew.
- For short intra-coastal voyages, a complete exchange may take too long to conduct before arrival (Lodge et al. 2006).
- Methods of MOE vary in their efficacy. The flow-through method, in which water is pumped through one portal and flows out of another, is generally less effective for a given volume than the empty-refill method, in which as much ballast is pumped out of the tank as possible, then refilled with ocean water (NRC 1996). These methods of exchange are described further in Chapter 3.
- Vessels with no ballast on board (NOBOB) pose a risk of invasions as the ballast tanks of these vessels contain residual water and sediments that may harbour AIS. These vessels may release AIS when the residual water mixes with new ballast water that is taken up when cargo is offloaded, and subsequently released in the surrounding environment when cargo is loaded.

Despite the above, MOE is the management practice most widely in use around the world, and it is considered to be generally effective in reducing the introductions of AIS in ballast water (Ruiz et al. 2007). However, quantitative assessments of MOE effectiveness are disparate and still incomplete (Ruiz et al. 2007).

1.3. BALLAST WATER MANAGEMENT

1.3.1. International

The International Maritime Organization is an international agency under the United Nations administering the International Convention for the Control and Management of Ships' Ballast Water and Sediments (2004). The convention stipulates a performance standard for ballast water treatment. Thirty states, representing 35% of world merchant shipping tonnage, are required to ratify the Convention before it enters into force (IMO 2004). To date, fourteen states (representing 3.6% of the world's gross tonnage) have ratified the convention (IMO 2008). Canada and the U.S. are currently not signatories to the Convention.

1.3.2. National

Canada introduced the Ballast Water Control and Management Regulations in June 2006, pursuant to the *Canada Shipping Act*, which are harmonized with the 2004 IMO Convention. Under the Regulations, all ships must treat or exchange (with 95% volumetric efficiency, or having replaced 95% of the tank volume) ballast water beyond 200 nautical miles from shore prior to discharge in Canadian waters (with some exceptions, including ships travelling exclusively intracoastally, and if the vessel's safety would be compromised), and must report to Canadian authorities. Vessels with NOBOB status must have either: a) previously conducted exchange 200 nautical miles from any shore and in water at least 2000 m deep prior to entering Canadian waters; or b) conducted saltwater flushing of empty ballast tanks at least 200 nautical miles away from any shore (flushing the unexchanged ballast and sediments in tanks with ocean water so that the salinity of the resulting mixture is greater than 30 parts per thousand) (Transport Canada 2006).

In the U.S.A., the National Invasive Species Act (1996) mandates ballast management reporting and provides voluntary MOE guidelines to vessels entering U.S. waters from outside the Exclusive Economic Zone (with the exception of military vessels, crude oil tankers that carry out coastwise trade, and some passenger ships that are equipped with ballast treatment systems). Recently, the U.S. Coast Guard proposed regulations requiring ballast water to be treated to the same standard as the IMO Convention. Within states, California has implemented the *Marine Invasive Species Act*, which, effective in March 2006, requires ballast management for all vessels operating within the Pacific Coast region. In 2002, the state of Washington implemented the *Ballast Water Management Act*, also requiring ballast management with some exceptions.

1.4. FACTORS OF ESTABLISHMENT SUCCESS

What causes an introduced species to become established in its new environment? Several hypotheses have emerged relating to how characteristics of a species, and how characteristics of a recipient ecosystem, can facilitate establishment success. Another emerging school of thought is propagule pressure, or the size and frequency of introduction events. These theories are described below.

1.4.1. Characteristics of invaders: Invasiveness

In attempting to identify future invaders, studies have investigated how the characteristics of the introduced species affect its establishment. These species-specific traits include growth rate, fecundity, taxonomic isolation, physiological tolerance, prior invasion success, trophic status, and abundance and range in its native habitat (Kolar and Lodge 2001; Langhoff 2002; Marchetti et al. 2004; Miller et al. 2002). For example, Grotkopp et al. (2002) found that the invasiveness of a species of pine was positively correlated to its relative growth rate, smaller seeds and shorter generation times. However, common traits between invasive species have only been found among a small group of species (Mack et al. 2000), and there are many cases in which an invasive species has relatives that are not similarly invasive, such as within the *Eichhornia* genus (water hyacinth) (Barrett 1989, as cited in Mack et al. 2000).

1.4.2. Characteristics of invaded communities: Invasibility

Numerous studies have also investigated how characteristics of an ecosystem can cause it to become vulnerable to invasions. These ecosystem variables include resource availability, community species richness, habitat suitability, whether there are vacant or under-utilized niches, and whether there are large-scale disturbances such as fires, floods, or changing nutrient dynamics (Langhoff 2002; Mack et al. 2000; Miller et al. 2002). Predicting the susceptibility of a community to invasions based on ecosystem variables, however, can be confounded by varying numbers of immigrants to ecosystems (Colautti et al. 2006; Mack et al. 2000). Factors related to invasion success may also depend on spatial scale: for example, studies conducted at small spatial scales show that diverse communities are highly resistant to invasion, but on a larger scale, diverse communities appear to be among the most invaded (Kennedy et al. 2002; Levine et al. 2000).

1.4.3. Propagule pressure

Propagule pressure is defined as the number of propagules (organisms) introduced in an introduction event, combined with the frequency of these events (Lodge et al. 2006). Propagule pressure has been recognized as an important factor in a species' establishment success (Lonsdale 1999; Von Holle and Simberloff 2005). Colautti et al.'s (2003) null model considers propagule pressure first in any investigation of factors relating to establishment success. In doing so, immigration biases are eliminated – in other words, particular species' or ecosystem traits are not mistakenly attributed to establishment success when propagule pressure is the actual cause. Relative to investigations of species-specific or ecosystem characteristics, there are fewer empirical studies examining propagule pressure (Colautti et al. 2006; Lockwood et al. 2005). This is due in part to the difficulty in quantifying the number of individuals arriving at a new location (Colautti et al. 2003; Mack et al. 2000). Data on the propagule pressure of AIS are especially lacking (Lodge et al. 2006; Perrings 2005). While several studies have demonstrated a positive relationship between propagule pressure and establishment success (i.e. Duggan et al. 2006), the nature of this relationship is as yet undetermined (Colautti et al. 2006; Kolar and Lodge 2001 and literature therein). Moreover, it is unclear that the simplification of propagule pressure as the number of individuals per introduction event multiplied by the number of events is appropriate – it may be that invasion success is a more complicated function of the two.

Propagule pressure can be estimated at three levels: potential, actual and effective (see Figure 1.1). Potential propagule pressure (PPP) is the coarsest level and uses vector or pathway characteristics as a proxy for direct quantification and identification of non-native species. For example, in the case of the shipping vector, ballast water volume discharges over time can be a measure of potential propagule pressure of AIS. Actual propagule pressure (APP) is a direct measure of the identity and quantity of organisms that are introduced to a given area. The number of introduced organisms that then go on to survive and produce viable offspring can be described as effective propagule pressure (EPP). EPP is a function of APP and the mortality rates of these organisms in their new environment.

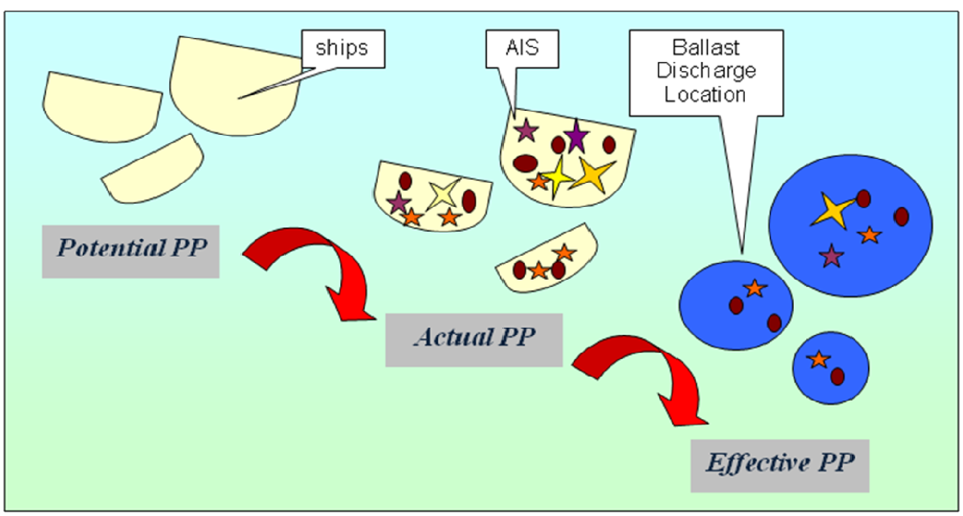

Figure 1.1: Three levels of propagule pressure (potential, actual and effective) of aquatic invasive species, adapted from the Canadian Aquatic Invasive Species Network, 2006

1.5. QUANTIFYING POTENTIAL AND EFFECTIVE PROPAGULE PRESSURE OF AIS

Propagule pressure of AIS has been estimated by modeling their dispersal patterns. Gravity models have recently been used to estimate the potential for dispersal of invasive species from source origins to their destinations. For example, Bossenbroek et al. (2001) predicted the spread of zebra mussels in inland lakes, and MacIsaac et al. (2002) forecasted the spread of *Bythotrophes longimanus* (spiny waterflea) in the Great Lakes, using empirical measures of abundance as well as vector flows obtained by surveying boaters, anglers and recreationalists. Environmental niche models have been also been used to estimate risk of invasion. For example, Herbourg et al. (2007) predicted the potential distribution of the Chinese mitten crab in North America by estimating the relative risk of invasion, using environmental similarity between ports and the volume of unexchanged ballast waters received.

For this thesis, I focused on estimating *potential* and *effective* propagule pressure. As a first estimate of propagule pressure, Colautti et al. (2003) used arrival data as a proxy for propagule pressure of AIS in the Great Lakes, with the assumption that ballast discharges were uniform for all ship arrivals. With the availability of comprehensive shipping data, however, it is possible to determine with greater accuracy the volumes and locations of ballast discharges. I quantified ballast discharge volumes over space and time to estimate potential propagule pressure for Canadian ports, using information obtained from ballast-water reporting forms that are required to be submitted to Canadian authorities before entry into Canadian waters (Ballast Water Control and Management Regulations, TC 2006). I also quantified potential propagule pressure of hull fouling species by using calculations of average wetted surface area for the vessels in my data set.

As ballast water discharge in a port for a given time period is a function of the number of vessels arriving in the port, arrivals are expected to be related to ballast discharge.

Similarly, since the total wetted surface of vessels arriving to a port is also a function of the number of arrivals, a positive relationship between the two is expected. Given that the amount of ballast discharged per voyage is variable due to numerous factors, including the amount of tonnage being transported and voyage weather conditions, I expected that arrivals would be better correlated with wetted surface area than ballast water. To test this, I investigated the relationship between arrivals, wetted surface and ballast water discharge across ports and vessel categories for different shipping regions. This work is summarized in Chapter Two of this volume.

Previous shipping analyses have been conducted only at local/regional scales. To our knowledge, this analysis of potential propagule pressure is the first of its kind in the world, and has important implications for management. Identifying ports/regions, ship categories, or seasons where propagule pressure is highest can aid in targeted AIS prevention measures. In addition, knowledge of the relationship between different measures of potential propagule pressure is useful where it is necessary to substitute one measure for another due to data limitations.

To estimate effective propagule pressure of ballast organisms, I added an environmental similarity term to a model created by MacIsaac et al. (2002), and incorporated my estimates of potential propagule pressure, as described above and in Chapter Two. I modeled the actual number of surviving individuals introduced to a shipping port, based on shipping data, species' mortality rates (as estimated using empirical work by Simard et al. in prep. and Gray et al. 2007), and environmental similarity between source and discharge ports. In this model, I assumed that the higher the similarity, the higher the survival of the species remaining in a tank after MOE. I explored different functions for this similarity-survival relationship, and the effect of using these functions on the final estimates of effective propagule pressure (EPP). It is expected that the shape of the relationship resembles a sigmoidal one, based on the reasoning that species at maximally similar or dissimilar ports will have uniformly similar invasion success. I determined the effects of changing the importance of different environmental variables in the similarity index on final organism densities. Presumably, EPP will be lower in ballast water that has undergone mid-ocean exchange. I tested this by determining the differences between EPP for exchanged vs. unexchanged ballast water.

This work, described in Chapter Three, has implications for policy and management of AIS. By applying the model to exchanged and unexchanged ballast water, we can determine theoretically the effectiveness of MOE and whether it meets national or international standards and regulations. Additionally, knowledge of how AIS abundance are affected by different environmental similarity indices, can aid in shaping policy directed at certain species or shipping ports/regions. This research can also be a starting point for investigating dispersal pathways (such as by using gravity or diffusion models), and invasion risks (as can be estimated through population viability analysis (PVA), or ecological niche modeling).

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2. QUANTIFYING POTENTIAL PROPAGULE PRESSURE OF AQUATIC INVASIVE SPECIES FROM THE COMMERCIAL SHIPPING INDUSTRY IN CANADA[1]

2.1. INTRODUCTION

Shipping is the primary source of unintentional introductions of aquatic invasive species (AIS) in North America (Ruiz et al. 2000). One estimate of the economic damage to the U.S.A. is $120 billion (USD), but this is conservative because it only includes the costs of prevention, detection and control efforts (Pimental et al. 2005). The impacts of AIS also include the depletion of fisheries and other resources, reduction in the quality of outdoor recreation, introduction of diseases, and secondary economic impacts stemming from human health effects and loss of biodiversity (Chapin III et al. 2000; Mack et al. 2002, Raaymakers 2002).

The uptake and discharge of ballast water for ship stabilization purposes has been recognized as one of the principle mechanisms of transporting AIS (Ruiz et al. 2000). Recent studies, however, demonstrate that hull fouling, which occurs when organisms attach to the vessel hull and other surfaces, are also an important source of AIS (Coutts et al. 2007), and can even pose a greater risk of species introductions than ballast water (Drake and Lodge 2007). Other possible commercial shipping vectors of AIS are resting egg stages of various organisms that reside in ballast water sediments (Bailey et al. 2005).

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Several hypotheses dealing with the factors involved in invasion success have been studied and tested, for example, characteristics of the recipient community or of the species itself, availability of spatial or nutrient resources, and previous invasion success (Colautti et al. 2003). One of the more recently-studied predictors of establishment success is propagule pressure, defined as the number of propagules in an introduction event, and the frequency of these events (Elton 1958; Lodge et al. 2006).

Propagule pressure can be classified as potential, actual or effective. The *potential* propagule pressure of AIS to a given site is a measure of the introduction effort; it is useful in the absence of AIS abundance data. For ballast water organisms, potential propagule pressure can be defined as the frequency and volume of ballast discharge, assuming that the number of AIS is proportional to the volume of ballast discharge. *Actual* propagule pressure is a measure of the number of organisms being introduced, which can be determined by enumerating organisms in ballast water, while *effective* propagule pressure is a measure of the proportion of introduced organisms that survive the entrainment process and produce viable offspring. The wetted surface area (WSA) of a vessel is an analogous measure of potential propagule pressure for hull fouling organisms and includes not only the hull, but other potentially colonizable surfaces such as propellers, rudders, sea chest gratings, bilge keels, bulbous bow, anchors and rope guards (Coutts and Taylor 2004).

Worldwide, ballast is generally managed by mid-ocean exchange (MOE). While other treatment technologies (e.g. McCollin et al. 2007; Quilez-Badia et al. 2008) are currently under development, many are not yet considered economically viable or technically feasible for most vessels (Drake et al. 2005; Ruiz 2007). Canada's Ballast Water Control and Management Regulations (effective June 28 2006), requires all vessels entering Canadian waters to conduct MOE beyond 200 nautical miles from shore, in waters at least 2000 m deep, provided it is safe to do so (Transport Canada 2006). Exceptions to this rule are vessels operating exclusively between ports in four areas: 1) on the west coast of North America north of Cape Blanco, Oregon; 2) on the east coast of North America, north of Cape Cod; 3) in the Bay of Fundy; and 4) on the east coast of Nova Scotia. Other exceptions are transoceanic “no ballast on board” or NOBOB vessels destined for the Great Lakes Basin, which do not carry ballast on board but have residual, often unpumpable ballast and sediment at the tank bottom. In the Great Lakes-St. Lawrence region, the majority (90%) of incoming arrivals are NOBOB (no ballast on board) ships (Grigorovich et al. 2003; Johengen et al. 2003), and subsequently are exempt from MOE but must conduct saltwater flushing.

Because ballast from NOBOBs are typically not exchanged and can be potentially transferred to ports during partial ballasting and de-ballasting, they pose a risk of AIS introductions. NOBOB vessels bound for the Great Lakes basin must therefore undergo saltwater flushing at least 200 nautical miles from shore before entering Canadian waters.

For hull fouling, the risk of AIS colonization has been reduced by using anti-fouling paint on vessel hulls. The use of tributylin (TBT), one of the most effective anti-fouling paints, is being phased out internationally due to toxicity concerns (Davidson et al. 2007). Unfortunately, the alternatives are not as effective. Hull fouling organisms can also be physically removed at dry-dock facilities, or in water, although the latter is not as effective and can actually make fouling worse (Davidson et al. 2007; Floerl 2005).

In our study we estimated the potential propagule pressure of AIS from shipping activities to Canadian ports, which, to our knowledge, is the first such analysis conducted on a nation-wide scale. Since the introduction of Canada’s ballast regulations, reporting of ballasting activities has been mandatory for all vessels entering Canadian waters. We used these comprehensive shipping data to estimate potential propagule pressure of AIS from ballast water on Canadian ports, using ballast discharge volume as a surrogate for the direct sampling of propagules. We estimated potential propagule pressure of hull fouling organisms by determining the total wetted surface area of the vessels in the ballast water database. Many vessels that pose a risk of hull fouling, such as small fishing vessels or recreational boats, were not recorded in the database as there were no ballast water reporting forms for those vessels.

Our objectives are the following:

1) Compare total wetted surface area, vessel arrivals and ballast discharge across shipping ports and vessel categories in the Atlantic, Great Lakes-St. Lawrence and Pacific shipping regions. We determine the shipping ports where the combined potential propagule pressure of hull fouling and ballast organisms is greatest. We investigate vessel arrivals and ballast discharge patterns across time. WSA was not included in this seasonal analysis because we lacked the data to determine the distribution of WSA across time. The following three objectives relate to ballast water:

2) Compare ballast management methods across shipping regions. The two major methods of MOE are empty-refill (ER) and flow-through (FT), also called dilution. In the former method, ballast is pumped out of a tank and subsequently refilled with ocean water. For FT exchange, ballast is pumped out while ocean water is simultaneously pumped in. An alternative management method is saltwater flushing (SWF), which involves rinsing the ballast tanks with ocean water so that the salinity of the resultant mix of residual water, sediments, and flush water is greater than 32 parts per thousand. Each method has a different efficacy, so knowledge of which methods are dominant will have implications for our understanding of potential propagule pressure across the three shipping regions.

3) Determine the origin of ballast water for the three shipping regions, to gain an understanding of the source of potential propagule pressure from ballast organisms.

4) Investigate the relationship between ships' gross tonnage and ballast water discharged: The accuracy of any estimate of invasion risk will depend on the resolution of ballast discharge data used. Worldwide shipping statistics are often given in the form of gross tonnage (GT), which is a measure of a vessel's volume. Measures of GT have

been used for the purposes of applying invasive species risk methodology (e.g. Harvey et al. 1999; Ruiz et al. 2007), as have measures of cargo tonnage (Leppäkoski and Gollasch 2006). However, actual ballast volume discharges give a more direct approximation of potential propagule pressure. These data have not been available at a high resolution in Canada until the introduction of the Ballast Water Control and Management Regulations, which mandate the submission of ballast reporting forms prior to entry into Canadian waters. To assess the accuracy of use of cargo tonnage statistics as proxies for ballast discharge, we therefore investigated the relationship between gross tonnage and reported ballast discharge volumes across several vessel types.

2.2. METHODS

2.2.1. Ballast water and vessel arrival data source

Shipping data were obtained in confidence from the Canadian Ballast Water Information System (BWIS), developed by the Department of Fisheries and Oceans Canada (DFO) and Transport Canada (TC). The BWIS is a repository for ballast water reporting forms that are submitted to Canadian authorities prior to arrival in Canadian waters. Prior to the implementation of the ballast regulations in June 2006, reporting of ballasting activities was only mandatory for some regions (e.g. Vancouver Port Authority, Great Lakes ports) and voluntary for most. Thus, we use data from forms submitted between November 2006 and October 2007, as this twelve month period represented the most comprehensive annual record of shipping data available for our analysis after the Canadian ballast water regulations were implemented. The degree of compliance with the new regulations is reportedly 97.5% for the Great Lakes-St. Lawrence region (Wiley, C., pers. comm., 2008), based on data obtained by officials from Transport Canada, the U.S. Coast Guard, and the Great Lakes-St. Lawrence Seaway. We thus assume that the data in the BWIS are representative of actual ballasting activities in Canada, and that there has been time for the shipping industry to adapt to and comply with the new regulations.

The data on the forms included ballast (volume taken up, exchanged and discharged), port names (arrival, ballast source, and discharge), date of arrival, vessel category, exchange method, and gross tonnage. Data in the BWIS were further analyzed using BallastScope, a query tool developed by DFO. The database includes both BOB and NOBOB vessels transiting the Great Lakes-St. Lawrence Region.

We grouped our data according to three major shipping regions in Canada: the Atlantic coast, GLSL and Pacific coast. Ports east of Quebec City were classified as Atlantic ports, as the limit of saltwater intrusion is usually at Quebec City or at Île D'Orléans, just west of Quebec City (Gobeil 2006). For the Pacific region, Vancouver Port, Roberts Bank and Port Moody were treated separately in our analysis, although they are all part of Port Metro Vancouver. Our analysis was conducted before Fraser Port joined with Port Metro Vancouver Port in 2008, so Fraser Port is also considered separately.

2.2.2. Estimation of wetted surface area

Since neither wetted surface area (WSA) values nor vessel dimensions were available for ships in our databases, we estimated WSA for vessels in the following manner. In brief, we obtained average WSAs for each vessel category, then calculated WSAs for individual ships based on the size of that ship relative to other ships in that category.

We obtained average WSAs for several ship categories from published results in Davidson et al. (2006), using the program Data Thief to extract relevant data. The formula used by the authors includes measures of vessel length, draft, and breadth, and various coefficients (presented in more detail in the Appendix). Davidson et al.

calculated WSAs for 5801 vessels arriving to ports on the Lower Columbia River, U.S.A., for vessel categories including bulk carriers, tankers, containers, car carriers ("roro" vessels in our analysis), barges, and "Other", which included passenger, research, naval, and fishing vessels, in addition to cable ships and other private craft. As we lacked data to repeat these calculations for our vessel data set, we used these published average WSA values for the ships in our arrival database, obtained from the BWIS.

For WSAs for individual ships, we modified these average values based on the ship's size (measured by gross tonnage) in relation to the variation in gross tonnage within vessel categories, using the following formula:

$$WSA = \mu_{wsa} + m\sigma_{wsa};$$

where μ_{wsa} is the mean WSA for the vessel category, σ_{wsa} is the standard deviation of WSAs for the vessel category (Davidson et al.'s data) =, and m is a measure of the ship's size relative to the vessel category given by the following:

$$m = \frac{GT - \mu_{GT}}{\sigma_{GT}};$$

where GT is the ship's gross tonnage value, μ_{gt} is the mean gross tonnage within the vessel class, and σ_{gt} is the standard deviation. Thus m can be negative and is effectively an individual vessel's gross tonnage relative size in its category, measured in number of standard deviations from the mean.

Average WSAs were not available for several vessel categories (chemical carriers, general cargo, reefer and passenger vessels). For these categories, we inferred WSA values from the categories represented in Davidson et al.'s (2006) study using our best estimates of the similarity of vessel categories in terms of mean gross tonnage and vessel shape. We did not use the mean WSA for barges as they were likely under-reported in the BWIS – only five vessels in the database were categorized as barges.

In applying these calculations, we assume that the mean WSA values in Davidson et al.'s (2006) data set are applicable to vessels in our data set—that the vessels arriving to the lower Columbia River are of similar size and shape to those arriving to Canadian shipping ports in our study regions. In applying our gross tonnage modifier to the mean WSA values, we also assume a linear, 1:1 relationship between WSA and gross tonnage.

Arrival and WSA data were categorized as: Class A - values reported in the shipping region, and Class B - reported arrivals to a shipping region, without a specific arrival port reported. Another class of vessels were those that arrived to ports outside Canada – these were not included in the analysis.

2.2.3. Data verification and analysis

There are two possible sources of error in the shipping data:

1) Reporting error, which is the incorrect reporting of data on forms. Reporting errors include inputting the incorrect methods of ballast exchange, spelling errors, using the wrong units, and incomplete entries. For example, there were many records indicating vessels arriving with ballast in tanks, but with zero ballast discharge reported in Canadian waters in the ballast water reporting form. Many of these vessels may have discharged ballast water at sea. Another possibility is that the vessel was transiting several ports (and thus discharged a small amount of ballast, loaded some cargo, and repeated this at another port), or perhaps the final destination port was unknown at the time the forms were required to be submitted (particularly in the case of the GLSL region).
2) Entry error, which is the incorrect transfer of data from the reporting forms to the BWIS. Entry errors include typographical errors, entering the same data

twice, and incomplete or inaccurate transfer of data into the BWIS due to illegibility of the forms.

While we could not remove both types of errors completely from the data before our analysis, several measures were taken to reduce their numbers. First, ship arrival dates were verified by a second person, and duplicate entries were removed. We conducted another verification of reported ballast water volumes by identifying outliers and determining whether it was likely that they were typographical errors. If so, we corrected the total ballast discharge from a particular vessel by using the average amount of ballast discharged per tank. Approximately 12 vessel discharges were corrected by this method.

We analyzed our data using a number of assumptions: 1.) If no ballast discharge port or discharge date were given we assumed it was the same as the arrival port or arrival date; 2.) If no ballast source port/date was given, it was assumed to be the same as the last port/date; and 3.) On some forms, discharge was reported for particular tank(s) but no volume was given (13822 entries, or 65% of the 39,010 total entries, 99.9% of which exchange had been indicated). A source volume was listed for 88% of the tank entries. In these cases, the discharge volume was assumed to be equivalent to the uptake volume for the particular tank – approximately 9400 tank entries were adjusted this way. To determine the representativeness of our data, we compared our results with previous shipping analyses. Below we attempt to account for discrepancies between various sources of data.

We used S-Plus version 8.0 software for statistical analyses (Insightful Corp. 2007).

2.3. RESULTS

2.3.1. Potential propagule pressure across shipping ports

The total number of vessels, wetted surface area and associated ballast discharges arriving to the Atlantic (40 ports), Great-Lakes St. Lawrence (21 ports), and Pacific (23 ports) region are summarized in Figure 2.1. Total ballast discharge for ports in each region are mapped in Figure 2.2a, b and c. By the number of arrivals, the three regions seemed quite similar with the Pacific region receiving the highest number (4129 arrivals). By WSA, the three regions are also quite similar but with the Atlantic region now receiving the highest percentage of WSA (43%). By ballast, there was a much greater difference between the regions, with the Atlantic region receiving considerably higher ballast volumes (2.3×10^7 *t*) than the Pacific region (1.6×10^7 *t*), and with the GLSL region receiving a much lower volume than both (1.7×10^6 *t*).

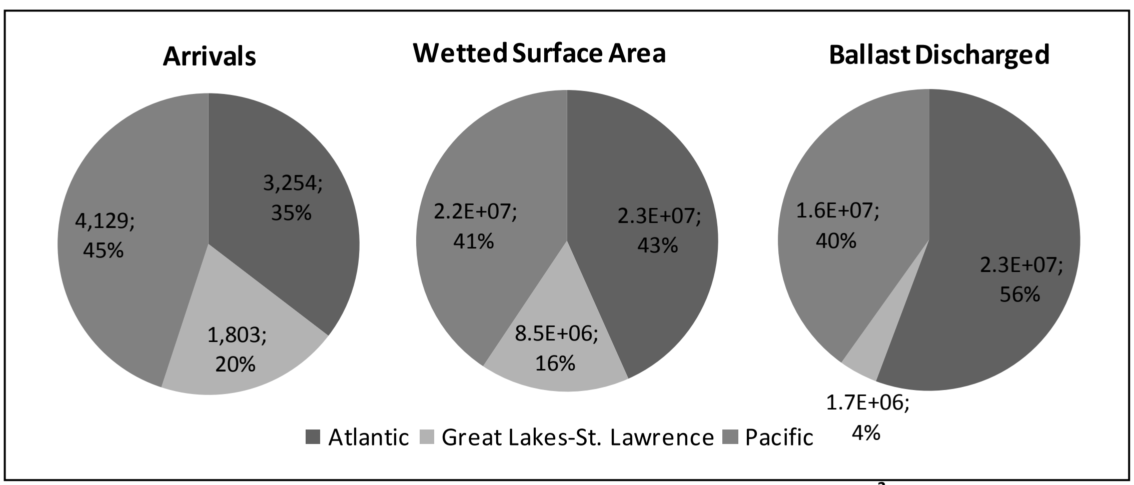

Figure 2.1: Total number of vessel arrivals, wetted surface area (mean value, m^3) and volume of ballast water discharged (*t*) to three Canadian shipping regions from November 1, 2006 to October 31, 2007.

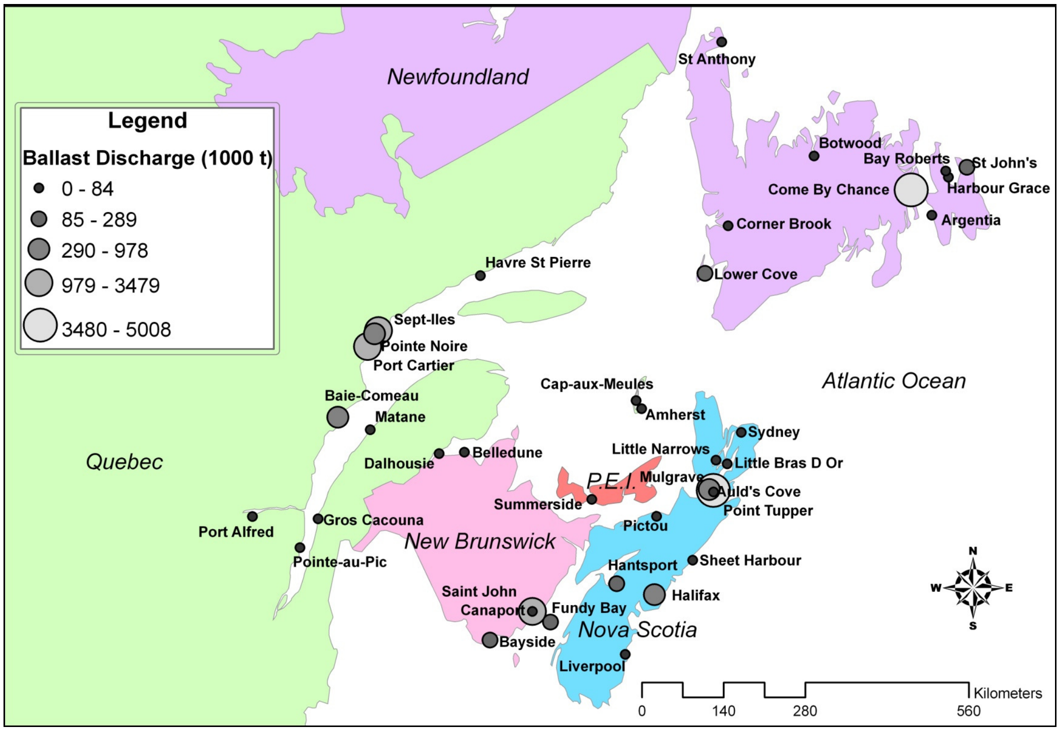

Figure 2.2a) Total ballast discharged in Atlantic shipping ports between November 1, 2006 and October 31, 2007. Ballast discharges for each port are indicated with proportional symbols. Ballast discharge volumes were classified using Jenk's natural breaks optimization method.

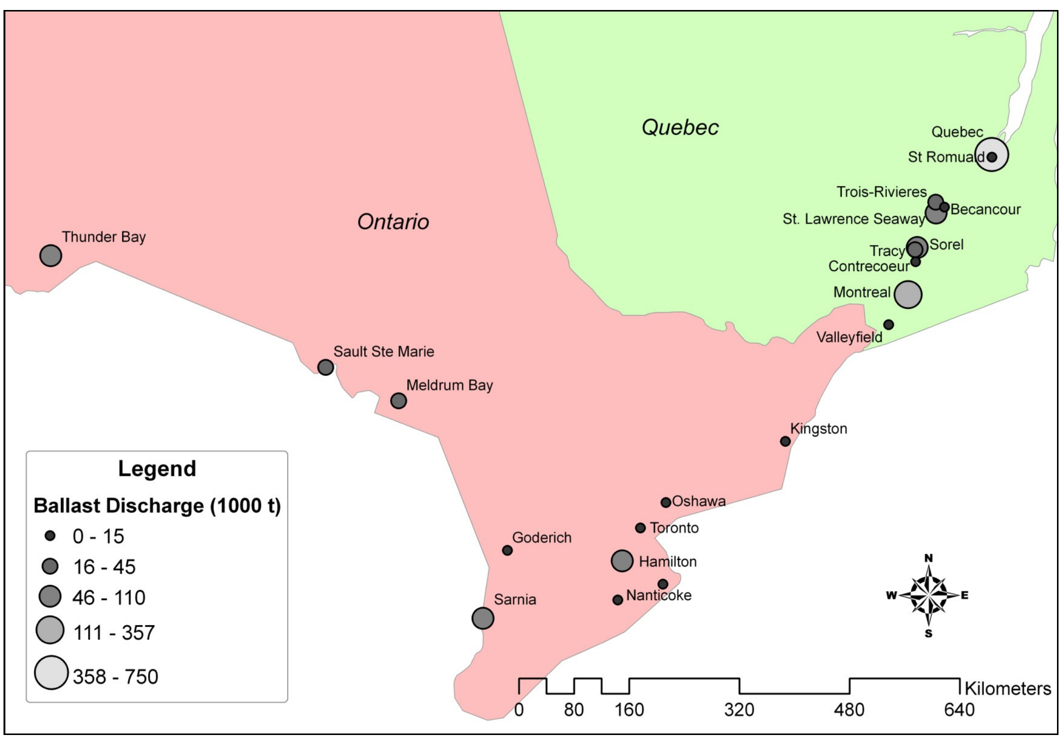

Figure 2.2b) Total ballast discharged in Great Lakes-St. Lawrence shipping ports between November 1, 2006 and October 31, 2007. Ballast discharge volumes were classified using Jenk's natural breaks optimization method.

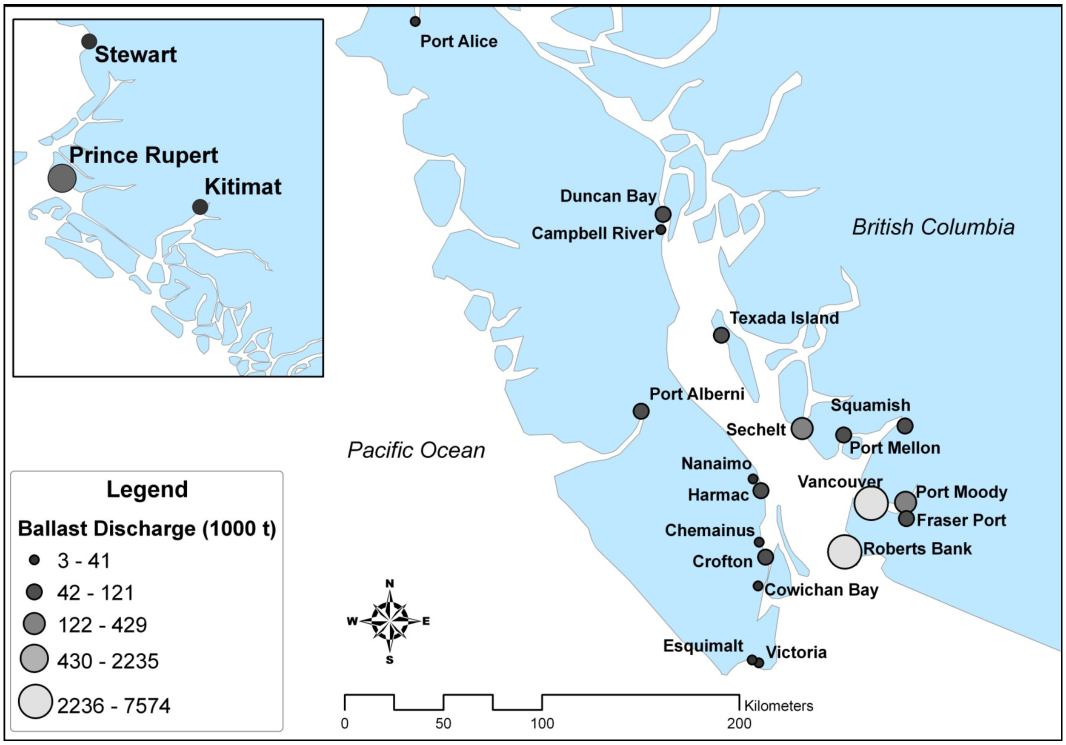

Figure 2.2c) Total ballast discharged in Pacific shipping ports between November 1, 2006 and October 31, 2007. Ballast discharge volumes were classified using Jenk's natural breaks optimization method.

The numbers of vessel arrivals, WSA, and ballast water discharges for each port considered in our analysis are listed in

Table 2.1. Ports with the highest percent total of WSA for the region did not always receive the most ballast, as can be seen with the ports of Halifax and Come by Chance in the Atlantic, and Montreal and Quebec in the GLSL. Ports that had a higher proportion of WSA relative to arrivals included Argentia, Canaport, Port Alfred and Sidney in the Atlantic region. Ports with the highest proportion of ballast discharge relative to arrivals included Meldrum Bay and Sault Ste. Marie in the GLSL.

The number of arrivals and volume of ballast discharge were significantly correlated across ports in each of the shipping regions (Table 2.2) Spearman's ρ = 0.81, 0.75 and 0.68, $p<0.01$ for the Atlantic, GLSL and Pacific shipping regions, respectively). Arrivals and WSA were highly correlated for the Pacific region (Spearman's ρ = 0.87, $p<0.0001$), but the correlations were lower for the Atlantic and GLSL region (Spearman's ρ = 0.73

and 0.76 respectively, p<0.0001). Correlations between WSA and ballast discharge were lower across all three regions (Spearman's ρ = 0.73, 0.57 and 0.67, p<0.01).

We used the chi-squared test to detect differences between propagule pressure type across ports, using the percent totals for arrivals, WSA and ballast water discharge. No significant relationship was found between arrivals, WSA and ballast discharge across ports (Atlantic: χ^2 (76, N = 117) = 81.7, p>0.05; GLSL: χ^2 (40, N = 63) = 55.2, p>0.05; Pacific: χ^2 (44, N = 69) = 56.6, p>0.05).

Table 2.1: Number of vessel arrivals, summed wetted surface area across all arrivals (WSA, m^2) and summed ballast discharges across arrivals (t) in Canadian shipping ports from November 1, 2006 to October 31, 2007. We lacked data to calculate WSA for certain ports, which we denote by "-". %Arrivals, %WSA and % Ballast refers to the percent total of arrivals, WSA and ballast across ports within a region. %WSA:%Arrivals and %Ballast:%Arrivals are the ratios for percent total arrivals to percent total WSA, and percent total arrivals to percent total ballast, respectively. 'Class B' Arrivals and WSA pertain to records of vessels arriving to unspecified ports in a shipping region.

Atlantic Region

Arrival Port	Arrivals	%Arrivals	WSA ($1000m^2$)	%WSA	%WSA: %Arrivals	Ballast (1000t)	%Ballast	%Ballast:% Arrivals
Amherst	1	0.1	-	-	-	14	0.1	1.0
Argentia	3	0.2	238	1.0	5.5	2	< 0.1	< 0.1
Auld's Cove	58	3.6	402	1.8	0.5	891	3.9	1.1
Baie-Comeau	74	4.6	517	2.3	0.5	553	2.4	0.5
Bay Roberts	7	0.4	1	< 0.1	< 0.1	1	< 0.1	< 0.1
Bayside	26	1.6	212	0.9	0.6	287	1.3	0.8
Belledune	20	1.2	208	0.9	0.7	41	0.2	0.1
Botwood	14	0.9	43	0.2	0.2	30	0.1	0.2
Canaport	4	0.2	337	1.5	5.9	15	0.1	0.3
Cap-aux-Meules	2	0.1	29	0.1	1.0	29	0.1	1.0
Come By Chance	163	10.2	1,791	7.8	0.8	4,414	19.5	1.9
Corner Brook	18	1.1	317	1.4	1.2	17	0.1	0.1
Dalhousie	41	2.6	132	0.6	0.2	53	0.2	0.1
Dartmouth	3	0.2	99	0.4	2.3	23	0.1	0.5
Fundy Bay	48	3.0	0	< 0.1	< 0.1	206	0.9	0.3
Grande-Anse	20	1.2	52	0.2	0.2	26	0.1	0.1
Gros Cacouna	7	0.4	45	0.2	0.4	8	< 0.1	0.1
Halifax	174	10.9	7,856	34.2	3.2	978	4.3	0.4
Hantsport	48	3.0	369	1.6	0.5	125	0.6	0.2
Harbour Grace	8	0.5	48	0.2	0.4	1	< 0.1	< 0.1
Havre St Pierre	4	0.2	17	0.1	0.3	24	0.1	0.4
Little Bras D Or	2	0.1	0	< 0.1	< 0.1	3	< 0.1	0.1
Little Narrows	6	0.4	110	0.5	1.3	48	0.2	0.6
Liverpool	2	0.1	10	< 0.1	0.3	1	0.0	< 0.1

Arrival Port	Arrivals	%Arrivals	WSA (1000m^2)	%WSA	%WSA: %Arrivals	Ballast (1000t)	%Ballast	%Ballast:% Arrivals
Lower Cove	30	1.9	171	0.7	0.4	289	1.3	0.7
Matane	5	0.3	16	0.1	0.2	6	< 0.1	0.1
Mulgrave	8	0.5	53	0.2	0.5	47	0.2	0.4
Pictou	4	0.2	7	< 0.1	0.1	11	< 0.1	0.2
Point Tupper	175	10.9	2,513	11.0	1.0	5,008	22.1	2.0
Pointe Noire	33	2.1	270	1.2	0.6	724	3.2	1.6
Pointe-au-Pic	13	0.8	33	0.1	0.2	19	0.1	0.1
Port Alfred	4	0.2	611	2.7	10.7	1	< 0.1	< 0.1
Port Cartier	99	6.2	841	3.7	0.6	2,280	10.1	1.6
Saint John	348	21.7	3,868	16.9	0.8	3,479	15.4	0.7
Sept-Iles	102	6.4	981	4.3	0.7	2,693	11.9	1.9
Sheet Harbour	5	0.3	38	0.2	0.5	84	0.4	1.2
St Anthony	6	0.4	40	0.2	0.5	5	0.0	0.1
St John's	11	0.7	196	0.9	1.2	206	0.9	1.3
Summerside	2	0.1	37	0.2	1.3	0	< 0.1	< 0.1
Sydney	5	0.3	442	1.9	6.2	17	0.1	0.2
Total	**1,603**		**22,951**			**22,660**		
Class B	1,921		7					
Grand Total	**3,524**		**22,958**			**22,660**		

Great Lakes-St. Lawrence Region

Arrival Port	Arrivals	%Arrivals	WSA (1000m^2)	%WSA	%WSA: %Arrivals	Ballast (1000t)	%Ballast	%Ballast:% Arrivals
Becancour	11	2.3	338	4.0	1.7	12	0.7	0.3
Contrecoeur	8	1.7	216	2.5	1.5	4	0.3	0.2
Goderich	4	0.8	7	0.1	0.1	2	0.1	0.2
Hamilton	18	3.8	219	2.6	0.7	73	4.3	1.2
Kingston	1	0.2	2	0.0	0.1	5	0.3	1.5
Meldrum Bay	2	0.4	15	0.2	0.4	35	2.0	4.9
Montreal	225	46.9	4,692	55.3	1.2	357	21.2	0.5
Nanticoke	3	0.6	76	0.9	1.4	15	0.9	1.4
Oshawa	5	1.0	16	0.2	0.2	2	0.1	0.1
Port Colborne	1	0.2	35	0.4	2.0	0	< 0.1	0.1
Quebec	82	17.1	1,759	20.7	1.2	750	44.4	2.6
Sarnia	25	5.2	129	1.5	0.3	74	4.4	0.8
Sault Ste Marie	1	0.2	24	0.3	1.4	18	1.1	5.2
Sorel	33	6.9	366	4.3	0.6	96	5.7	0.8
St Lawrence Seaway	4	0.8	37	0.4	0.5	1	0.1	0.1
St Romuald	2	0.4	38	0.4	1.1	45	2.7	6.4
Thunder Bay	29	6.0	90	1.1	0.2	110	6.5	1.1
Toronto	1	0.2	59	0.7	3.3	1	< 0.1	0.2
Tracy	2	0.4	8	0.1	0.2	26	1.6	3.7
Trois-Rivieres	22	4.6	320	3.8	0.8	60	3.5	0.8
Valleyfield	1	0.2	44	0.5	2.5	1	< 0.1	0.2
Total	**480**		**8,489**			**1,688**		
Class B	1,323							
Grand Total	**1,803**		**8,489**			**1,688**		

Pacific Region

Arrival Port	Arrivals	%Arrivals	WSA (1000m^2)	%WSA	%WSA: %Arrivals	Ballast (1000t)	%Ballast	%Ballast:% Arrivals
Campbell River	2	0.1	33	0.2	1.7	7	< 0.1	0.4
Chemainus	15	0.7	10	< 0.1	0.1	12	0.1	0.1
Cowichan Bay	14	0.6	20	0.1	0.1	32	0.2	0.3
Crofton	73	3.4	217	1.0	0.3	121	0.7	0.2
Duncan Bay	23	1.1	75	0.3	0.3	57	0.4	0.3
Esquimalt	3	0.1	9	< 0.1	0.3	3	< 0.1	0.1
Fraser Port	104	4.8	1,954	9.1	1.9	238	1.5	0.3
Harmac	26	1.2	91	0.4	0.4	60	0.4	0.3
Kitimat	24	1.1	282	1.3	1.2	52	0.3	0.3
Nanaimo	14	0.6	101	0.5	0.7	20	0.1	0.2
Port Alberni	22	1.0	63	0.3	0.3	53	0.3	0.3
Port Alice	8	0.4	7	< 0.1	0.1	17	0.1	0.3
Port Mellon	37	1.7	55	0.3	0.2	64	0.4	0.2
Port Moody	14	0.6	59	0.3	0.4	76	0.5	0.7
Prince Rupert	159	7.3	1,033	4.8	0.7	2,235	13.7	1.9
Ridley Island	2	0.1	17	0.1	0.9	41	0.3	2.7
Roberts Bank	177	8.2	1,515	7.0	0.9	5,016	30.7	3.8
Sechelt	27	1.2	162	0.8	0.6	429	2.6	2.1
Squamish	63	2.9	193	0.9	0.3	77	0.5	0.2
Stewart	18	0.8	43	0.2	0.2	48	0.3	0.4
Texada Island	6	0.3	44	0.2	0.7	88	0.5	1.9
Vancouver	1328	61.3	14,253	66.2	1.1	7,574	46.4	0.8
Victoria	129	5.6	1,281	6.0	1.1	4	< 0.1	< 0.1
Total	**2288**		**21,517**			**16,323**		
Class B	1,841							
Grand Total	**4,129**		**21,517**			**16,323**		

2.3.2. Potential propagule pressure across vessel categories

Arrivals, wetted surface area, and ballast discharge were significantly correlated with each other across vessel categories within each of the three regions (See Spearman's ρ values in Table 2.2, $p<0.05$)

Table 2.2: Spearman's correlation values for arrivals, WSA; arrivals, ballast; and WSA, ballast across shipping ports and across vessel categories in three major shipping regions. All correlations were significant ($p<0.05$), with some exceptions which are marked with an asterisk.

Shipping Region	Arrivals, WSA	Arrivals, Ballast	WSA, Ballast
Correlations Across Ports			
Atlantic	0.73	0.81	0.73
Great Lakes-St. Lawrence	0.76	0.75	0.57
Pacific	0.87	0.67	0.67
Correlations Across Vessel Categories			
Atlantic	0.93	0.64	0.52*
Great Lakes-St. Lawrence	0.83	0.98	0.79
Pacific	0.98	0.52*	0.43*

For each region, bulkers and tankers accounted for the majority of ballast water discharge (Table 2.3). In the Atlantic region, bulkers and tankers together made up roughly half of arrivals (54%) and WSA (57%). However, they accounted for the majority (95%) of ballast discharge. In contrast, in the GLSL region, the combined number of arrivals and WSA from bulkers and tankers (47.2 and 52.8%) were more similar to the share of ballast discharged from these vessel categories (67.2%). In the Pacific region, bulkers made up roughly a third of arrivals and WSA (37 and 33%, respectively), while they accounted for the majority (82%) of total ballast discharge. Fewer tankers arrived in the Pacific (6% of total) compared to the other regions (27% in the Atlantic region and 21% in the GLSL region).

Another important vessel category is container ships, which contributed 29% of total arrivals, 35.4% of total WSA, and 12% of the total ballast discharged in the GLSL. Container ships were the second and third highest sources of WSA for the Pacific and

Atlantic regions, respectively. In contrast, only 0.3 and 1.7 % of total annual ballast discharged was associated with container arrivals in the Atlantic and Pacific.

Table 2.3: Arrivals, Wetted Surface Area, and Ballast Discharged (% Total) by Vessel Category

	Bulker	Tanker	Other	General Cargo	Container	Chemical	Roro	Combo	Passenger	Reefer
Atlantic										
Arrivals	26.9	27.2	4.1	8.9	18.6	1.5	6.5	0.6	4.6	1.3
WSA	28.9	28.1	2.3	2.6	25.0	1.4	4.7	0.6	6.2	0.2
Ballast	39.6	54.9	1.9	1.6	0.3	1.1	0.6	0.1	0.0	0.0
Great Lakes - St. Lawrence										
Arrivals	26.6	20.6	1.7	17.0	27.8	3.0	0.5	0.5	2.3	0.0
WSA	30.3	22.5	1.0	4.2	35.4	2.8	0.3	0.2	3.2	0.0
Ballast	47.9	19.3	8.8	7.2	12.2	3.6	0.7	0.2	0.1	0.0
Pacific										
Arrivals	37.1	6.0	5.0	14.1	16.9	2.9	7.8	2.4	7.8	0.0
WSA	33.4	4.7	2.6	6.5	28.7	2.1	5.5	0.6	15.9	0.0
Ballast	81.9	3.7	5.5	5.0	1.7	0.4	0.8	1.0	0.0	0.0

2.3.3. Potential propagule pressure across time assessed with ballast water data

The correlation between the number of arrivals and the total volume of ballast water across months were significantly higher for the Atlantic and Pacific regions (Spearman's ρ = 0.9, p<0.001; and ρ = 0.82, p = 0.01, respectively) than for the GLSL shipping region (Spearman's ρ = 0.64, p = 0.049) (Figure 2.3**:** Vessel arrivals and ballast discharged in Canada between November 2006 – October 2007 for the (a) Atlantic, (b) Great Lakes-St. Lawrence and (c) Pacific shipping region. Solid bars indicate ballast discharge (10 000 t), and the solid line indicates the number of monthly arrivals.). Total volumes of discharge and number of arrivals varied between regions, as did seasonal patterns of discharge and arrivals. Shipping activity decreased from May to July for the Atlantic region, but increased in the following months of August and September. In the GLSL region, shipping activity was highest from August to October, approximately corresponding to the ice-free shipping season. In the Pacific region, shipping activity was relatively evenly distributed through the months, although it decreased slightly during winter.

The number of arrivals in the Pacific region was similar in winter, spring and summer. In the summer, the Pacific had a peak in arrivals reported, whereas the Atlantic had a marked downturn. The Great Lakes region generally received fewer arrivals than the other two regions, with the lowest number of arrivals occurring in December, January and February, corresponding to the St. Lawrence Seaway's non-navigable season (Great Lakes St. Lawrence Seaway System website, 2008). The amount of ballast discharged in this region followed a more variable pattern, and was lowest between November to February, and April.

In terms of ballast discharged, the Atlantic region received the greatest volumes overall, but was exceeded by the Pacific region throughout April to July.

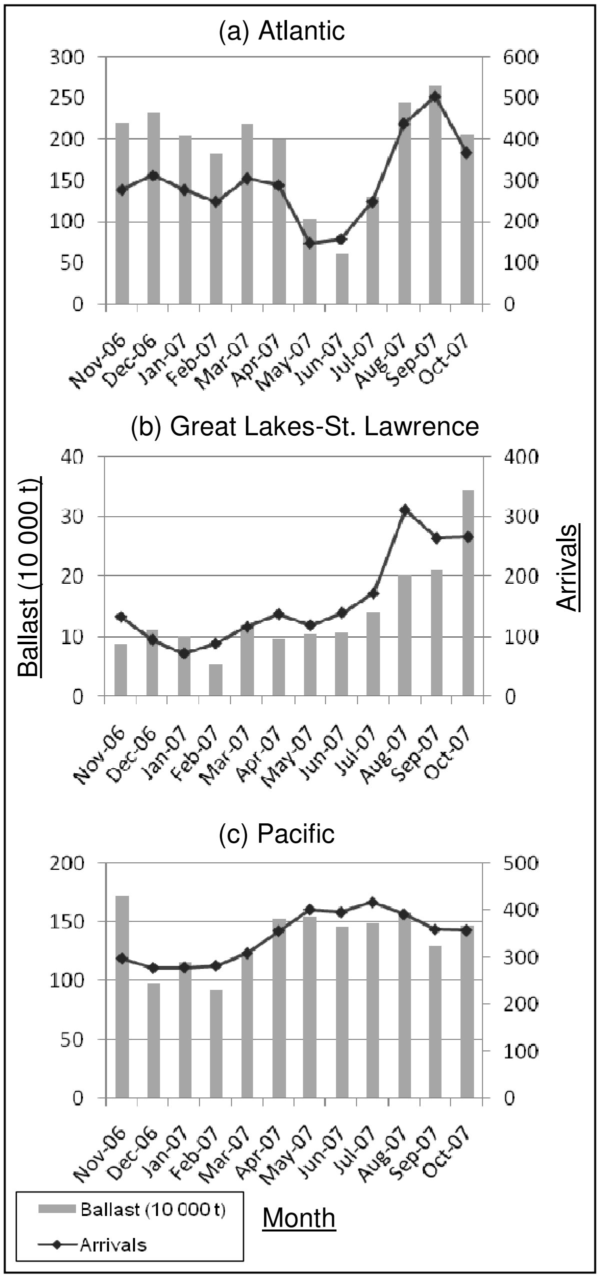

Figure 2.3: **Vessel arrivals and ballast discharged in Canada between November 2006 – October 2007 for the (a) Atlantic, (b) Great Lakes-St. Lawrence and (c) Pacific shipping region. Solid bars indicate ballast discharge (10 000 t), and the solid line indicates the number of monthly arrivals.**

2.3.4. Management of ballast water across shipping regions

Results of our analysis showed that ballast water management methods were similar for ships discharging ballast in the Atlantic and Pacific shipping regions (Figure 2.4). 65 and 67% of the ballast discharged had been exchanged by the FT method, while 35 and 32% had been exchanged by the ER method for the Atlantic and Pacific, respectively. For the Great Lakes, 37 and 58% of ballast had been exchanged via the ER and FT methods, respectively. Another 5.5% was classified as "alternative", while no vessels selected SWFas a method. The definition of "alternative" is unclear in the instructions for filling out the forms. Consequently it is possible that exchange methods may have been misclassified as "alternative" when SWF was actually conducted.

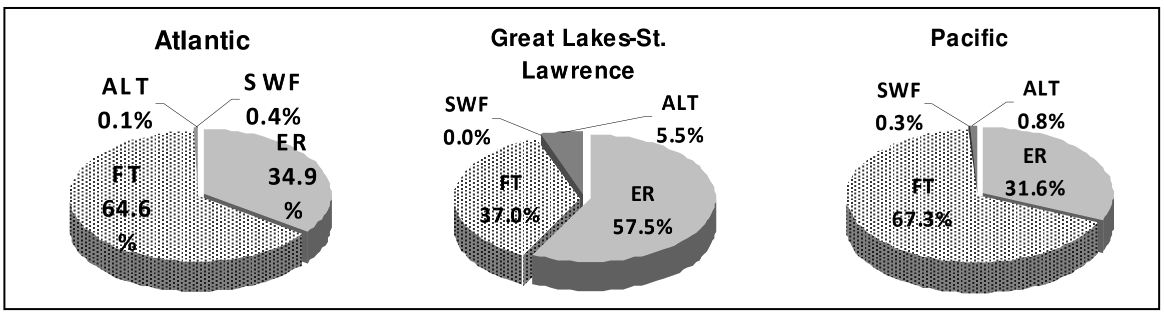

Figure 2.4: Ballast management methods in major Canadian shipping regions. ALT = alternative exchange method, ER=empty-refill, FT=flow-through, SWF=saltwater flushing

2.3.5. Ballast water origin across shipping regions

Ballast water origins for each shipping region are listed in

Table 2.4. A map of source ports for each shipping region is illustrated in Figure 2.5. In the Atlantic region, 64% of ballast originated from coastal ports along the eastern coast of the U.S., and 6.2% originated from Canada. The rest originated from various European ports. In the Great Lakes-St. Lawrence, about 40% of discharged ballast originated from the U.S. (22.5%) and Canada (19.3%), with the rest coming from European ports. In the Pacific region, ballast origin was dominated by northeast Asian ports (47.2, 11.7 and 10.4% from Japan, South Korea and China, respectively). 14.2% originated from ports on the west coast of the U.S., while the rest originated from various ports in Canada, Mexico, South and Central America, Cuba, and Southeast Asia.

Table 2.4: **Origin of Ballast Water Discharged to the Atlantic, Great Lakes-St. Lawrence and Pacific region**

Atlantic			Great Lakes-St. Lawrence			Pacific		
Origin	***Volume (1000 t)***	***% Total***	***Origin***	***Volume (1000 t)***	***% Total***	***Origin***	***Volume (1000 t)***	***% Total***
USA	14471	63.9	USA	380	22.5	Japan	7711	47.2
Netherlands	2136	9.4	Canada	325	19.3	USA	2316	14.2
UK	1763	7.8	UK	207	12.2	China	1902	11.7
Canada	1399	6.2	Belgium	82	4.9	S. Korea	1693	10.4
Spain	448	2.0	France	72	4.2	Canada	202	1.2
Belgium	280	1.2	Netherlands	68	4.0	Mexico	167	1.0
France	245	1.1	Spain	50	3.0	Taiwan	128	0.8
Denmark	198	0.9	Italy	50	2.9	Philippines	63	0.4
Germany	175	0.8	Denmark	29	1.7	Guatemala	40	0.2
Puerto Rico	91	0.4	Ireland	27	1.6	Chile	31	0.2
Italy	83	0.4	Germany	24	1.4	El Salvador	30	0.2
Ireland	73	0.3	Israel	10	0.6	Costa Rica	20	0.1
Indonesia	68	0.3	Russia	9	0.6	Cuba	18	0.1
Romania	67	0.3	Iceland	9	0.5	Ecuador	16	0.1
Algeria	64	0.3	Venezuela	8	0.5	Thailand	14	0.1
Other	1099	4.9	Other	339	20.1	Other	1972	12.1
Total	**22660**			**1688**			**16323**	

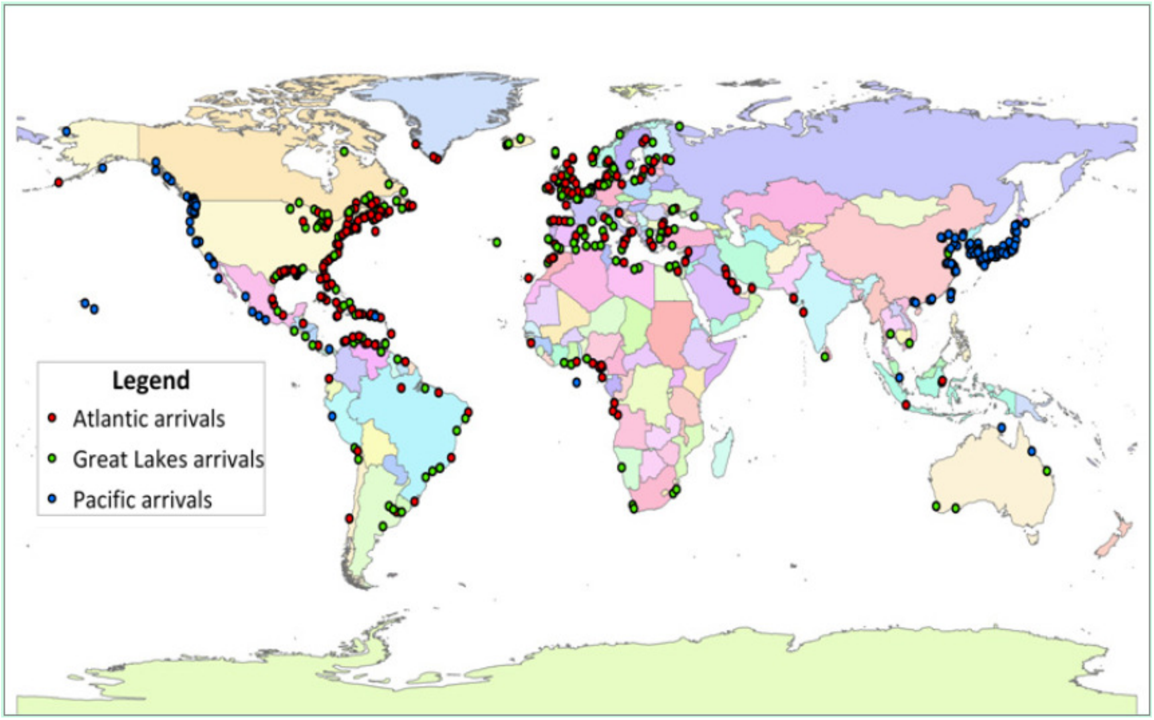

Figure 2.5: Locations of ballast water origins for ballast discharged at ports in three Canadian shipping regions (Atlantic, Great Lakes-St. Lawrence, and Pacific), from Nov. 2006 to Oct. 2007.

2.3.6. Relationship between gross tonnage and ballast water discharge across vessel categories

Our results indicate a statistically significant linear relationship between ballast discharge volumes and gross tonnage for bulkers, tankers and general cargo vessels (linear regression, $p<0.0001$ for all three cases) (Figure 2.6). Most of the variance in ballast discharge across ship-voyages can be explained by the ship's gross tonnage for bulkers (R^2=0.86) and tankers (R^2=0.82), but the coefficient of determination is much weaker in general cargo vessels (R^2=0.19).

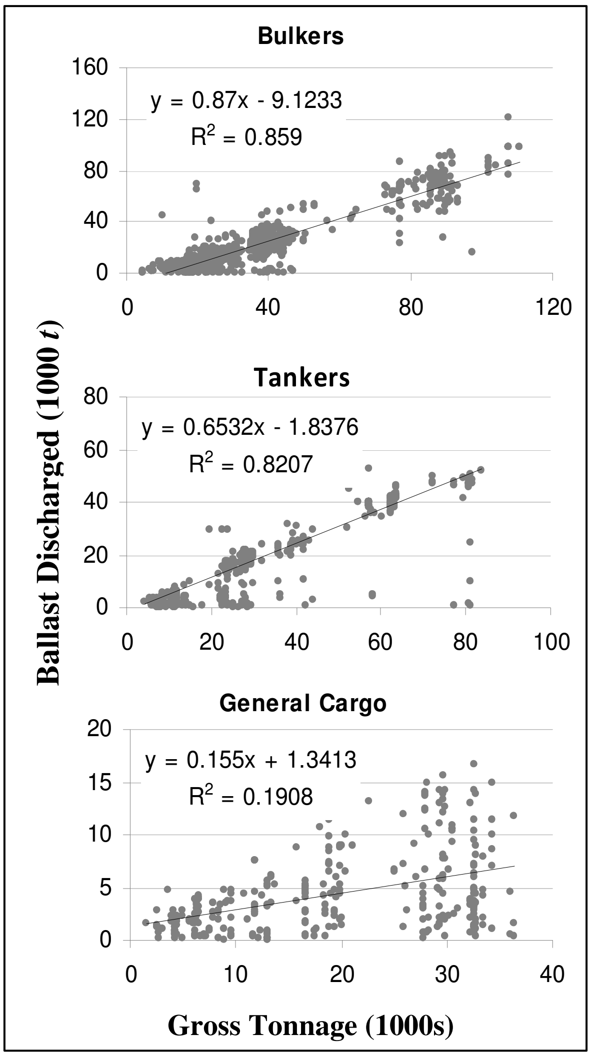

Figure 2.6: Volume of ballast discharged (*t*) vs. gross tonnage for three vessel categories: bulk carriers, tankers and general cargo ships.

2.4. DISCUSSION

To our knowledge, this is the first national-scale analysis of potential propagule pressure for hull fouling and ballast organisms from the commercial shipping sector. Analyses of arrivals and ballast water discharge have previously been conducted only at regional scales (e.g. Gramling 2000; Balaban 2001, McGee et al. 2006, Humphrey 2008). We have also estimated potential hull fouling propagule pressure across Canada in a novel way, by quantifying WSA in relation to a vessel's gross tonnage.

Our preliminary estimates of potential propagule pressure for ballast and hull fouling organisms demonstrate that ballast discharge and WSA estimates are correlated across ports - but more so for Atlantic ports than GLSL or Pacific ports. Arrivals, a coarse proxy for hull fouling and ballast organisms, were highly correlated to both WSA and ballast discharge across ports by roughly the same degree. Arrivals are a better predictor of WSA across vessel categories than across ports, an expected result due to the influence of the shape of different types of vessels on WSA. Ballast discharge, on the other hand, can vary greatly for any vessel. Arrivals were most poorly correlated with ballast discharge for the Pacific region both across ports and vessel categories. These results demonstrate that arrivals are not always a good proxy for ballast discharge and WSA. However, for the regions showing high correlations, arrival data can be used as an indicator of potential propagule pressure in the absence of WSA or ballast water data, as arrival data are easier to obtain.

Our estimate of propagule pressure of AIS introduced by ballast water is coarse, as it does not account for other factors that mediate survival, such as the method and volume of ballast exchange, voyage duration, and environmental and life history parameters. Similarly, while WSA may serve as a rough proxy for hull fouling, a more accurate estimate requires accounting for several other factors. These factors include voyage length, vessel speed (high speed vessels may deter the ability of AIS to colonize on hulls), whether the hull is treated with anti-fouling paints, and the history of dry-docking activities, among other factors (Davidson et al. 2006).

These results have implications for current research on propagule pressure, raising the question of how actual and effective propagule pressure of hull fouling and ballast organisms relate to each other. On a management level, preliminary estimates of potential propagule pressure can be used to determine high-risk areas that can potentially be targeted for further AIS prevention and control measures. Where comprehensive data on ballast discharge are limited, arrivals may be a good indicator of propagule pressure of ballast organisms, and a better indicator of propagule pressure of hull fouling organisms. However, our results should be interpreted with some caution as they depend on a number of assumptions that we have outlined above and discuss below.

2.4.1. Comparisons with other shipping analyses

We compared results from our study to previous shipping analyses for Canadian coastal regions, although we note that these other studies use different regional classifications of ports and sources of data. Several ports included in our analysis are not included in these other studies, and vice versa.

While actual hull fouling propagule pressure has been measured empirically (e.g. Darbyson et al. 2009; Mineur et al. 2008), and effective hull fouling propagule pressure has been estimated with environmental niche models (i.e. Herborg et al. 2009), there are few analyses of potential propagule pressure in our shipping regions for which we can compare our results.

As Davidson et al.'s mean WSA values were calculated from 5801 vessels covering a range of different categories, we believe our assumption of similar distributions of vessels (as outlined in the Methods) is reasonable.

Our second assumption, as mentioned above, is that gross tonnage is linearly related to WSA. As gross tonnage is a measure of a vessel's volume, which indirectly influences WSA, we have reason to assume that there is a positive relationship between the two, although the shape of this relationship has not been determined and is an area for further research.

2.4.2. Ballast water and arrival comparisons

2.4.2.1. *Atlantic region*

We reported 3524 arrivals to the Atlantic coast. This is a lower number than reported by Balaban (2001), who documented 5504 vessels from foreign ports of origin arriving at Canadian ports on the Atlantic coast. This author also reported that vessel traffic was dominated by tankers, containers, general cargo and bulkers. The reason for our lower estimate is probably due to the fact that commercial fishing and recreational vessels were not included in our analysis, as they are not a significant source of ballast water. No ballast reporting forms were submitted for vessels arriving to Yarmouth and various other ports where there is a high concentration of fishing vessels. In terms of source ports, Balaban (2001) reported that the USA, UK, Spain and the Netherlands accounted for approximately 62%, 5%, 4% and 4% of the total ballast discharged to the East coast, respectively, which corresponds closely with the source ports we identified for the Atlantic region (see
Table 2.4).

2.4.2.2. *Great Lakes-St. Lawrence region*

We estimated total ballast discharge as 1.7×10^6 t, higher than our previous estimate of 0.9×10^6 t in 2005, using the same data source (Lo et al. 2007). Not all data from 2005 had been entered into the BWIS (Santavy, S. pers. comm. 2008), which may explain the discrepancy; however, it may also be a reflection of the new Canadian ballast reporting requirements. We found that the majority of reported discharges were in Quebec or Montreal (~44 and 21 % of total volume, respectively), while 6.5% occurred in Thunder Bay, Lake Superior.

Our data suggest that European ports contribute the most ballast water to the GLSL region. Of total ballast, 0.4×10^6 *t* (19%), originated from the GLSL itself, particularly from the port of Montreal. Ruiz et al. (2007) determined that half or more of ballast discharged to the Great Lakes region (not including the St. Lawrence Seaway) originated from Western Europe and the Mediterranean Sea, followed by North and South America. Prior to entering the Great Lakes, Western Europe is the most common location where recent ballasting has occurred prior to vessels entering the Great Lakes, with the Great Lakes themselves being the second most common region where recent ballasting has occurred.

2.4.2.3. *Pacific Region*

While there were more arrivals in the Pacific region than in the Atlantic, there was a higher volume of ballast discharged into the Atlantic region. As suggested by our results in Table 2.3, it appears that the majority of ballast was discharged by tankers in the Atlantic, and by bulkers in the Pacific.

For the November 2006 – October 2007 time period, our data shows 1328 arrivals in Vancouver port, from 793 vessels, representing 70.9×10^6 GT. With the addition of Port Moody and Roberts Bank, which are considered part of Port Metro Vancouver but are geographically separate, the figure rises to 1501 arrivals. Higher numbers have been reported in other studies - Niimi et al. (2000) reported that the port of Vancouver (including Port Moody and Roberts Bank) received 2595-2795 overseas visits from 1202 to 1292 vessels annually between 1995 and 1997. Gramling (2000) reported 2743 vessel calls (91.2×10^6 GT) in Vancouver in 1998, also with the inclusion of Roberts Bank and Port Moody data. Bulk cargo volume shipped through the Vancouver Port were similar from 1996-1998 and 2006-2007 (time period for BWIS data), whereas the total volume of cargo shipped through the Port of Vancouver has actually increased in that time period (Port of Metro Vancouver 2008). Our results show a lower number of arrivals than previous studies, possibly because not all ballast reporting forms were entered into the BWIS, and not all vessels on the West Coast were fully in compliance with the Canadian ballast reporting requirements.

In terms of source ports, our data show that most of the ballast water discharged to the Pacific region originated from Japan, South Korea, China, and Taiwan, in that order. Levings (1998) and Gramling (2000) noted similar ballast origins for Vancouver, but also identified Brazil, Great Britain, Indonesia, and Italy as major ballast contributors. A study of AIS abundances in Vancouver harbour by Humphey et al. (2008) demonstrated that in terms of actual propagule pressure, intracoastal unexchanged ballast from U.S. ports contained greater species densities than exchanged intracoastal ballast or exchanged foreign ballast. The unexchanged ballast water therefore represented higher actual propagule pressure relative to exchanged ballast water, even though the latter showed much higher potential propagule pressure.

2.4.3. Ballast water management

Our estimate of potential propagule pressure of AIS in ballast water does not account for whether exchange was conducted, or what method of exchange was used. Ballast exchange methods are significant in determining potential propagule pressure as each method has an associated biological efficacy, or efficacy of removal of AIS. This efficacy also depends on other factors, such as the volume of water exchanged, tank type, and chemical and biological water properties (Wonham et al. 2001, Ruiz and Smith 2005, Choi et al. 2005).

Our analysis demonstrates that both FT and ER are major exchange methods for ballast discharged in Canada. FT is the dominant exchange method on the east and west coasts, while ER is dominant in the Great Lakes-St. Lawrence region. While FT exchange requires more time (due to the requirement of exchanging 300% of the tank's volume), it is a safer method of exchange as the vessel can maintain stability throughout, unlike ER, where all of the source water is pumped out before being refilled with ocean water. This may explain why FT is dominant on both coasts of Canada, as transoceanic voyages typically take longer than coastal voyages. However, FT has also been demonstrated to be less effective than ER (Cordell et al 2008). ER appears to be the preferred method of exchange for ships discharging ballast to the Great Lakes-St. Lawrence region. It is possible that ships traversing the St. Lawrence River have less time to conduct exchange via the FT method and thus prefer ER.

2.4.4. Relationship between gross tonnage and ballast discharge

Our analysis showed that while gross tonnage can be a reliable indicator for ballast water discharge for bulkers and tankers, it is likely a poor proxy for potential propagule pressure for general cargo vessels. Generally, bulkers deliver one type of cargo such as coal or grains directly to their destination ports, as do crude oil tankers (BMT Fleet Technology Limited 2008). Container ships may visit a few ports from their origin before calling at North American ports (BMT Fleet Technology Limited 2006a), so they release variable amounts of ballast water per visit, as do other vessel types (Ro-Ro and general cargo). General cargo ships are multi-purpose vessels that handle a variety of cargo, including forest products, machinery, or manufactured goods. Discharge volumes for general cargo ships are thus more variable than bulkers and tankers, which may explain the lower correlation in the linear relationship between gross tonnage and ballast discharge for this vessel category.

Our results agree with the findings of Harvey et al. (1999), who demonstrate a statistically significant relationship between ballast water and gross tonnage for both bulkers and general cargo vessels, and that the correlation is weaker for the latter vessel category.

2.4.5. Data Quality

We made a number of assumptions about our data in order to conduct our analysis, We assume that all information was correctly reported and inputted. Input error was reduced via data verification at Transport Canada, but the accuracy of the actual reporting is unknown. BMT Fleet Technology (2006 a, b and c), who also used ballast reporting forms in their studies, reported inconsistencies in shipping databases by different agencies, suggesting a "significant gap between the ship movements recorded by administrative bodies and the actual ship movements." Their analysis took place prior to mandatory reporting requirements, however. Thus, the data from the reporting forms used in our analysis are the best estimate so far of ballast water volumes available in Canada after the implementation of the ballast water regulations, which mandate the submission of ballast water reporting forms. Because many of the ballast water reporting forms were incomplete, we lacked ballast discharge volumes for many vessels and thus assumed that the volume of ballast taken up at the source port was equivalent to what was discharged. While not all vessels discharge all the ballast in their tanks, a subset of the forms for which we had complete ballast water data showed that the majority of vessels had indeed discharged roughly the same volume that was taken up at the source port. To avoid making these assumptions, accurate reporting of ballast discharge volume and other fields in the ballast water reporting forms are important for future analyses of propagule pressure from the commercial shipping sector.

It is evident that, while there is broad agreement between our results and the results of previous shipping studies, some inconsistencies exist, probably due to differences in data sources, port classification systems, annual variation in shipping patterns, and human error in data entry. In the case of the BWIS, data from ballast reporting forms are manually entered into the database. As noted by BMT Fleet Technology Limited (2006a, b and c), an automated system may reduce data transfer error. This system has recently been developed; however, the majority of vessel officers still submit forms via e-mail or fax, necessitating personnel to manually enter the data into the database (Santavy, S. pers. comm. 2008).

We note that our port classification scheme differs from others. The Great Lakes-St. Lawrence Seaway, managed by the U.S. and Canada, includes the ports of Baie Comeau, Port Cartier and Sept-Îles, which are classified as Atlantic ports in our analysis. A shipping analysis by BMT Fleet Technology (2006 a, b and c) also groups these ports, as well as Amherst, Belledune, Cap-Aux-Meules, Dalhousie, Matane, Pointe-au-Pic, and Port Alfred as within the Great Lakes-St. Lawrence region. We identify these particular ports as Atlantic ports in our analysis, as they are more similar in salinity to the other Atlantic ports. We assume this salinity difference creates biological, rather than administrative, boundaries in our port classification system. The propagule pressure data presented here can thus be used with biological theory to investigate factors in the establishment success of particular AIS species in different shipping regions.

2.5. CONCLUSION

This study is a first attempt at quantifying potential hull fouling and ballast water propagule pressure of AIS in Canada from the commercial shipping industry. Our results show that the potential propagule pressure of hull fouling organisms and ballast water organisms, as measured by vessel arrivals, wetted surface area, and ballast discharge, are significantly correlated ($p<0.01$) across ports and vessel categories. The degree of correlation, however, differs by shipping region. Similarly, no significant differences were found between different types of potential propagule pressure across ports for each of the regions. The high traffic volume from recreational boaters and fishing vessels on the east coast add further to the hull fouling potential propagule pressure of the other vessel categories represented here.

We identified key pathways of potential propagule pressure, or top shipping ports that receive the highest quantities of ballast water and hull fouling. These include Point Tupper, Come By Chance, Halifax, Saint John and Sept Îles for the Atlantic region;

Quebec, Montreal, Thunder Bay and Sorel for the Great Lakes St.-Lawrence region; and Vancouver, Roberts Bank, Prince Rupert and Fraser or for the Pacific region. In terms of vessel categories, bulkers and tankers discharged the majority of ballast to each region, although in the Pacific region, bulkers discharged a larger proportion than tankers.

Ballast management methods were not uniform across Canada – in the Atlantic and Pacific regions, flow-through exchange was dominant (64.6 and 67.3%, respectively), while empty-refill was more common in the Great Lakes-St. Lawrence region (57.3%).

Gross tonnage can be a poor indicator of ballast water discharge. Although there is a strong relationship between gross tonnage and ballast for bulk carriers and tankers, gross tonnage can be misrepresentative of ballast discharged by general cargo vessels.

As shipping traffic increases worldwide, the importance of ballast water and hull fouling as vectors for AIS will also increase. In this study, we quantified the potential propagule pressure of AIS from the commercial shipping vector and demonstrate how they relate across ports, vessel categories, and seasons for three major shipping regions in Canada. These results are significant for policy and management of AIS. Prevention and detection measures can be targeted at ports and regions that receive higher amounts of propagule pressure. Additionally, caution should be employed when substituting some measures of PPP, such as gross tonnage and arrivals, for others, such as ballast discharge volumes. Improved ballast data quality and compliance measures for Canada's ballast water regulations will be important for achieving accurate analyses of potential propagule pressure. Further studies relating potential propagule pressure to actual and effective propagule pressure will increase our understanding of the factors underlying the establishment success of AIS.

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3. MODELING EFFECTIVE PROPAGULE PRESSURE OF AQUATIC INVASIVE SPECIES: A CASE STUDY OF CANADIAN PORTS[2]

3.1. INTRODUCTION

The impacts of invasive species on ecosystems are extensively documented and include disruption of species interactions, alteration of nutrient cycles and the physical features of an ecosystem, introduction of pathogens and diseases, and damage to fisheries (Chapin III et al. 2000; Lodge et al. 2006; Mack et al. 2000; van der Velde et al. 2006). All of these impacts necessitate spending on prevention and control: annually, the cost to protect Great Lakes fisheries by controlling the invasive sea lamprey is $10 - 15 million (National Council for Science and the Environment 1999), and the cost of introduced disease organisms to human, plant and animal health in the U.S. is estimated at $41 billion (Daszak et al. 2000).

The establishment success of invasive species depends on a number of different factors. A major factor is propagule pressure, defined as the number of propagules in an introduction event and the frequency of these events (Lodge et al. 2006). In the case of aquatic invasive species introduced via ballast water of ships, *potential* propagule pressure to shipping ports can be defined as the volume of ballast discharged and the frequency of discharge, *actual* propagule pressure is the abundance of organisms in the ballast water, while *effective* propagule pressure is the abundance of viable organisms after discharge. Other factors in invasion success include the difference in environmental conditions between the uptake and exchange locations, mortality throughout the voyage (a function of voyage length), and colonization and successful reproduction once organisms are released to their new environments (Carlton 1996; Smith et al. 1999), which can be thought of as *realized* propagule pressure.

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The most widespread method of ballast water management is mid-ocean exchange (MOE), although numerous efforts are underway to develop ballast treatment technologies (e.g. Boldor et al. 2008, de Lafontaine et al. 2007). During MOE, the coastal ballast water taken up at a port is replaced with ocean water. MOE has been mandatory for ships entering Canadian waters since June 2006, when Transport Canada implemented the Ballast Water Control and Management Regulations (Transport Canada 2006), which require exchange beyond 200 nautical miles from shore (with the exception of ships operating exclusively along parts of the coast).

Numerous studies on the effectiveness of exchange have been conducted (e.g. Levings et al. 2004; Ruiz and Reid 2007; Wonham et al. 2001). Although results vary, the general trend from these empirical studies is that MOE is effective in reducing the risk of invasion to freshwater and estuarine ports (Ruiz and Reid 2007). However, invasion risk *increases* if euryhaline organisms (those that can tolerate a wide range of salinity) survive exchange. This may occur, for example, when trade is between marine ports, or if organisms taken aboard at the exchange site (Wonham et al. 2005). Policy to reduce the risk of aquatic invasion would benefit greatly from an understanding of the relative importance of MOE and other factors related to propagule pressure.

Methods of risk assessment in use or in development can be broadly categorized as using a species/taxon-specific approach or an environmental similarity approach (Barry et al. 2008). An example of the former is a theoretical model created by MacIsaac et al. (2002), which quantifies the abundance of individuals of a taxon deposited by a single voyage by including species' mortalities, voyage duration, and initial densities as variables. An example of the latter is the Ballast Water Risk Assessment (BWRA) tool developed by the International Maritime Organization (IMO) (2004). This tool creates an index quantifying the risk of introduction of AIS to a given port from a particular source port, effectively summing across species and voyages. The index includes a measure of environmental similarity between source and discharge ports, vessel arrival data, and the presence of potentially invasive species present in source ports. Environmental similarity in terms of salinity regimes has been demonstrated to affect the survival of ballast organisms (Hines and Ruiz 2000; Ruiz et al. 2007; Smith et al. 1999), and similarity indices have recently been used as predictive tools for species' occurrences (e.g. Herborg et al. 2007).

The species-specific approach requires comprehensive data on a target species' life history traits, presence/absence data, and physiological tolerances to changes in environmental variables. To our knowledge, existing species-specific models have not yet accounted for the impact of the source port's physical and chemical characteristics on organism survival at the discharge port. The environmental similarity approach requires a careful selection of environmental variables that are relevant to invasion risk (Barry et al. 2008), and their summary nature makes it impossible to tease apart contributions by species or voyages. Some of these models do not incorporate information on ballast water exchange and discharge patterns, and how they differ by vessel category.

The abundance model we propose in this paper includes both environmental similarity (between source and destination ports), and species-specific parameters. The model is built on the above-mentioned work by MacIsaac et al. (2002), and it incorporates the impact of environmental similarity between source and discharge ports on mortality rates. We parameterized the model with empirical data collected from ship-board ballast water studies in order to calculate mortality rates for several ballast water zooplankton species. We focused mainly on copepods, as they are widely documented as the most abundant zooplankton in ballast tanks (e.g. Gollasch et al. 2000; Lavoie et al. 1999; Smith et al. 1999). There are more data available on copepod density in ballast water than on other ballast organisms such as rotifers. However, as the species we modeled are not known to be invasive in Canada, we assume invasive species will behave like the cosmopolitan ones we modeled.

Our model provides a mechanistic, empirically-informed estimate of effective propagule pressure. In the case of AIS introduced through shipping activities, only potential propagule pressure has been estimated - by using shipping characteristics such as ballast volume discharges (as in Colautti et al. 2003), or direct sampling of ballast water (as in Verling et al. 2005). With the availability of comprehensive shipping data, however, it is possible to determine with greater accuracy the volumes, dates and locations of ballast discharges, types of mid-ocean exchange conducted, size of tanks, etc. (i.e. Lo et al. in prep). Thus, for a shipping port at a particular time, we can calculate a reasonable estimate of effective propagule pressure by parameterizing the theoretical model proposed by MacIsaac et al. (2002) with most comprehensive data on ballast discharges available on a nation-wide scale, and incorporating an index of source-destination similarity. Using these data enables us to avoid assuming values for variables critical to invasion success, such as the assumption that mortality rates will be the same for different copepod species, or that the five-day survival rate of organisms is two orders of magnitude lower in saltwater than freshwater (as in MacIsaac et al. 2002).

In this paper, we apply our modeled mortality rates to quantify total effective propagule pressure of zooplankton discharged from ballast water in Sept-Îles, Hamilton and Vancouver (representative ports for the Atlantic, Great Lakes St. Lawrence (GLSL) and Pacific shipping regions, respectively), across all ship types. We determine how mid-ocean exchange and variation in average daily mortality rates affect final modeled abundances. We also determine the sensitivity of our model to changing both the function and the weighting of variables for the source-destination environmental similarity index.

3.2. METHODS

3.2.1. Model development

We build upon a model developed by MacIsaac et al. (2002), which predicts the density *n* of invasive species, taxon *i,* discharged alive in a tank *j* at the time of ballast discharge *D* (see Equation 3.1). We modified the model by incorporating an environmental similarity index (S_{sd}) that describes the similarity of source (*s*) and discharge (*d*) port physical environments. With increasing values of S_{sd}, which corresponds to greater similarities of port environments, we assume in our model that there will be increased per-capita survival and final densities. We represent this relationship between similarity and survival as a sigmoidal one, as most species likely have uniformly very low survival in environments that are very different from the environment from which they came (across a wide range of environmental difference), and most likely have uniformly high survival in environments quite similar (again over a range of values of environmental difference). However, the response of a species at particular life stages to environmental gradients may be described by other functions, across time and space. We explore these relationships in a sensitivity analysis, described below. The model (Equation 3.1) parameters are described below and summarized in Table 3.1.

Equation 3.1: *Final Density*

$$n_{ijD} = n_{ij0}(1-r_1)e^{-u_1 t_{sx}} e^{-u_2 t_{xd}} r_2 \frac{1}{1+e^{-a(S_{sd}-0.5)}}$$

Given comprehensive shipping data on ballast volume discharges per tank, we can calculate the total number of individuals released by each vessel *k* (Equation 3.2), where *Q* is the total number of tanks, and v_j is the total ballast volume for a tank *j*. Total propagule pressure for a taxon *i*, in a given destination port for a given time period can then be estimated by taking the sum of final densities across *M* vessels for port *P*, as in MacIsaac et al. (2002) (Equation 3.3).

Equation 3.2: *Total Per-Vessel Abundance*

$$N_{ikD} = \sum_{j=1}^{Q} n_{ij0} v_j (1 - r_1) e^{-\mu_1 t_{sx}} e^{-\mu_2 t_{xd}} r_2 \frac{1}{1 + e^{-a(S_{sd} - 0.5)}}$$

Equation 3.3: *Total Per-Port Abundance*

$$N_{iDP} = \sum_{k=1}^{M} N_{ikD}$$

Table 3.1: **Description of model parameters and data sources. ER = Empty-refill, FT = Flowthrough, SWF = Saltwater flush, BWIS = Ballast Water Information System, TC-Transport Canada, DFO = Fisheries and Oceans Canada**

Parameter	Description	Data Source
N_{iDP}	Total number of surviving individuals of taxon *i*, across tanks, discharged in ballast water for a port *P*	Model, Equation 3.3
n_{ij0}	Initial organism density (individuals per metric tonne of ballast water), for taxon *i* in tank *j* at time *0* (at the start of the voyage)	Empirical data (Simard et al. in prep; Gray et al. 2007)
μ_1, μ_2	Survival rate before exchange (μ_1) and after exchange (μ_2)	Empirical data (Simard et al. in prep; Gray et al. 2007)
$1-r_1$	Probability that an organism will be retained in the ballast tanks during exchange (with r_1 being the probability that it is discharged during exchange)	ER: Assumed 99% (Rigby and Hallegraeff 1994, Wonham *et al*. 2005) FT: Exponential function modified from Rigby and Hallegraeff 1994 (calculations in Appendix) SWF: Assumed 98% (MacIsaac et al. 2002)
r_2	Probability that an organism will be discharged during ballast discharge	Calculated per tank using ratio of ballast discharged to ballast uptake; data from the BWIS (TC and DFO)
S_{sd}	Environmental similarity index , calculated by using values for environmental variables (temperature and salinity)	Environmental data from the IMO Globallast Program, 2004. Index for a particular source and discharge port calculated by using the Euclidean distance between two sets of environmental variables (calculations in Appendix)
a	Constant; modifies the effect of S_{sd}	
t_{sx} , t_{xd}	Time in days from point of uptake to exchange (t_{sx}) and time from point of exchange to discharge (t_{xd})	BWIS and BallastScope (DFO)
v	Volume of ballast discharged (in metric tonnes)	BWIS and BallastScope (DFO)

3.2.1.1. Probability of organism retention ($1-r_1$)

The probability of an organism being discharged after MOE (r_1), and thus its probability of retention ($1-r_1$), can vary across ballast management methods and ship types. Management methods include MOE by empty-refill (ER, or sequential) and flow-through (FT).

Empty-refill (ER), or sequential exchange, occurs by removing ballast water first, then refilling the tank with mid-ocean water, so that 100% of the original volume of water is replaced. Effectiveness of organism removal after exchange (r_1) is approximately 99% for bulk carriers when it is conducted at 100% tank removal (Ruiz *et al.* 2007). We adopted this value for our model as the best estimate of effectiveness that we are aware of. As data on the ER efficiency for other ship types are lacking, we used the same assumption of 99% discharge efficiency.

FT exchange is conducted by continually pumping in ocean water while overflowing the ballast tanks. Approximately 95% of ballast organisms will be discharged after a 300% tank volume replacement, assuming that organisms behave like inanimate particles (NRC 1994). As the reported amount of FT tank volume replacement varied from approximately 30 to 800%, we fitted an exponential function to obtain measures of efficacy, based on a study by Rigby and Hallegraeff (1994) who used dye tracers to evaluate efficacy on a bulk carrier (described in Appendix).

Saltwater flushing (SWF) is another method of ballast management for ships that declare "no ballast on board" (NOBOB), and are thus exempt from mid-ocean exchange. Any ships discharging unexchanged residual ballast water (typical of vessels frequenting Great Lakes waters) are required to perform SWF by taking up mid-ocean water to mix with the residual, so that the resulting salinity is over 30 parts per thousand (Transport Canada 2006). We could not obtain data on the biological efficacy of saltwater flushing for zooplankton species, so we employed the same assumption of a 98% efficiency for NOBOB ships (the majority of which conduct SWF) as did MacIsaac *et al.* (2002).

3.2.1.2. Probability of organism discharge after ballast discharge (r_2)

The probability of an organism being discharged when the ship deballasts at destination is influenced by several factors including ballast water mixing conditions, the motility of the target species, and the proportion of ballast water discharged in relation to the total volume of ballast water taken up at the source region. As sufficient data are lacking to account for the first two factors, we assume that that r_2 is equivalent to the third (ballast water discharged), effectively assuming that species are well-mixed in the ballast water. We expect that this assumption will result in r_2 being over-estimated for some organisms (e.g., nekton and some meroplankton, organisms that have swimming capabilities and can move to avoid being discharged) and possibly underestimated for others (i.e. non-motile algae).

3.2.1.3. Initial ballast water organism density (n_{ijD})

We draw upon empirical studies of ballast water organism densities over time to obtain n_o, initial densities per *t* (metric ton) of ballast water, and estimates of average daily mortality rates for species found in ballast tanks. Ballast organism densities were obtained from Simard *et al.* (in prep) who sampled ballast water from a bulk carrier bound for Sept-Iles, Quebec (on the Gulf of St. Lawrence, Atlantic coast of Canada), arriving in September 1999, from Rotterdam, the Netherlands. The zooplankton species we analyzed from this voyage were the copepods *Paracalanus parvus*, *Acartia clausii*, *Oithona minuta*, *Oithona similis*, and *Euterpina acutifrons* (see Table 3.3 for taxonomic information). We also obtained data from a study by Gray *et al.* (2007), who sampled ballast water from cargo ships bound for Cartagena, Spain (arriving in October 2004) and Hamburg, Germany (arriving May and August, 2005 and December, 2006) from Hamilton, Ontario (in the Canadian Great Lakes-St. Lawrence (GLSL) shipping region).

The zooplankton species we analyzed were *Mesocyclops edax*, *Diacyclops thomasi*, *Bosmina coregoni*, *Daphnia mendotae*, and *Polyarthra vulgaris* (see Table 3.3). These studies were selected because they included species-specific densities after ballast uptake and discharge, for control and exchanged tanks.

3.2.1.4. Initial (pre-exchange) and final (post-exchange) mortality rates

μ_1 (initial mortality rate) and μ_2 (final mortality rate) were obtained by solving for their values in the following exponential decay function (as in MacIsaac et al. 2002):

Equation 3.4: *Initial and Final Mortality Rates*

$$n_{ij}(t) = n_{ij0} e^{-\mu t}$$

where for μ_1, n_{ij0} is the initial density of taxon *i* in tank *j* at time *0* at the ballast uptake port, $n_{ij}(t)$ is the final density of taxon *i* at the end of the voyage before discharge, and *t* is the time in days between ballast uptake and discharge. Similarly, we obtained μ_2 by applying the function to organism densities in exchanged tanks, using the initial density (n_{ij0}) after exchange was completed and final density (n_t) on the final day of the voyage. Here we follow MacIsaac et al. (2002) in assuming that mortality is constant over time and that no reproduction occurs.

We obtained two sets of data to calculate species mortality rates: one set representative of species in the Atlantic region, and another set representative of species in the GLSL region. There was a lack of available data to calculate mortality rates for the Pacific coast, so we applied the species mortality rates calculated for the Atlantic region to our analysis of propagule pressure for the Pacific region (with our assumptions described below).

For the Atlantic region, μ_1 and μ_2 were obtained by using average organism densities from two control and two exchanged tanks (using the data provided by Simard et al., in prep). In the GLSL shipping region, μ_1 was obtained by averaging 3 samples each for initial and final densities in the control tank (using data provided by Grey et al. 2007). We were unable to obtain μ_2 because no samples were taken after MOE. Given the other parameters of the model (see Equation 3.1) we solved for μ_2, using the average of the initial densities from the control and exchanged tanks as our value for n_{ij0}. We provide a summary of formulae for mortality rates and error calculations in the Appendix.

3.2.1.5. Error estimates for mortality rates

Mortality rates for the Atlantic voyage were calculated by using the average abundance of organisms taken from two tanks (one sample per tank). Error estimates were not provided for these data, so we calculated a coefficient of variation (CV) (ratio of standard deviation to the mean) for densities to approximate sampling error, effectively assuming constant mortality across the voyage, i.e., that sampling and inter-tank variation were the only sources of variation (see Appendix for calculation methods). These error values were propagated using methods described in Taylor et al. (1997) (see Appendix) to obtain a measure of standard error for the mortality rates.

Initial mortality rates for the GLSL region were calculated by using the average abundance taken from three samples, each from a single tank. We propagated the error values provided by Gray et al*.* (2007) to obtain sampling errors. The initial error values given were both sample standard deviations, and also confidence levels based on their assumption that the vertical distribution of zooplankton in a ballast tank follows a Poisson distribution.

We tested our assumption of constant mortality for the Atlantic voyage by comparing CVs across regions (Atlantic and GLSL) and species. We used a Mann-Whitney U-test to compare the relative ranking of the CVs between the two regions. In calculating CVs for the Atlantic region (which we use to estimate the standard deviation and thus the sampling error), we assumed constant mortality, whereas the sampling error for the Great Lakes was provided. Thus, a significant difference in CVs between regions may be interpreted as evidence that mortality rates vary with time within a voyage for the Atlantic region.

3.2.1.6. Source-discharge environmental similarity index (S_{sd})

We obtained environmental data for 599 worldwide ports from the Ballast Water Risk Assessment (BWRA) tool developed by the IMO. These data were gathered from a variety of sources including scientific, government and port publications, sampling records, survey reports, and climate databases and atlases (IMO 2004). We used four water temperature variables (mean and highest during summer, and mean and lowest during winter), and four salinity variables (mean and lowest during wet periods and mean and highest during dry periods) to calculate environmental similarity, S_{sd}, between ports.

Euclidean distances are a standard metric of environmental similarity measured on multivariate environmental variables (Barry et al. 2008). This metric has been used, for example, to determine the effect of environmental variation on community species composition (i.e. Jones et al. 2006), and it has been adopted by the International Maritime Organization for their Ballast Water Risk Assessment Tool (International Maritime Organization 2004). We calculated the standardized (mean = 0 and standard deviation = 1) Euclidean distance from Sept-Îles, Hamilton and Vancouver (on Canada's Pacific coast) to all ports worldwide for which we have environmental data (599 ports in total). The Euclidean distances we computed were normalized to a 0–1 similarity index, with 1 representing a perfect environmental match, and 0 representing the highest degree of dissimilarity in the dataset (calculations in Appendix). We assume that the environmental conditions between two ports can be dissimilar enough so that no propagules introduced from one port to another will be able to survive, hence S_{sd} will be 0. Euclidean distances were thus normalized relative to the maximally dissimilar source port (of all the 599 ports) for a given destination port. We test two other major assumptions in a sensitivity analysis (described below): that temperature and salinity variables are equally important in determining effective propagule pressure, and that there is a sigmoidal relationship between invasion success and environmental similarity for all species in our analysis, although this relationship may vary between species, time and space.

3.2.2. Total effective propagule pressure

We modeled total effective propagule pressure, or the sum of all EPP over ballast water discharges by ships, for one port from each shipping region. We used the above parameters (Table 3.1) in combination with shipping data provided by Fisheries and Oceans Canada (DFO) and Transport Canada (TC). The two federal agencies developed the Ballast Water Information System (Transport Canada 2006), a repository for shipping data extracted from ballast water reporting forms that ship officers are required to submit to Canadian authorities as of the June 2006 Regulations. We compiled data from November 1, 2006 to October 31, 2007 for all vessels discharging ballast water to Sept-Iles, Hamilton, and Vancouver. For each ballast tank of a vessel, the data included the volume of ballast discharged, type of exchange conducted, percentage tank replacement by MOE, source ports, and dates of uptake, exchange and discharge.

We modeled the final densities of surviving individuals per tank using the above data and parameters from Table 3.1 and multiplied each density by the volume discharged to arrive at the total abundance of organisms discharged per tank, which were summed to give the total per annum abundance of viable organisms discharged into the ports of Sept-Iles and Hamilton, which are the ports that the empirical data from Simard et al. (in prep) and Gray et al. (2006)are based on. Our estimates are made with the assumption that the conditions of the specific voyages in which density data were collected by Simard et al. (in prep) and Gray et al. (2007) are representative of the voyage conditions (across tanks, ships and seasons) for all voyages to Sept-Îles and Hamilton.

We were unable to calculate mortality rates for species being brought to the Pacific region due to a lack of data. Therefore, we used the mortality rates calculated for the Sept-Îles voyage in the Atlantic region to model total effective propagule pressure for the Pacific region (in combination with Pacific shipping data and environmental similarity). We applied the mortality rates for the copepod species *Euterpina acutifrons*, *Paracalanus parvus*, *Oithona similis*, and *Acartia clausii* as the first three taxa have been found in the ballast tanks of ships arriving to the Pacific region (Humphrey 2008; Levings et al. 2004), while the fourth has been found in ballast water of vessels arriving in nearby Pacific waters in the U.S. (Cordell et al. 2007) and is considered to have a worldwide distribution (Karanas et al. 1979). We also used the mortality rate for *O. minuta*, as calculated for the Sept-Îles voyage, as it is considered a eurythermal species, and is widely distributed in the Black Sea and Atlantic Ocean (Monchenko 1998; Berdnikov et al. 1999), and could thus hypothetically survive in Pacific waters with similar environments. As above, by applying these mortality rates, we assume that the voyage conditions of ships arriving to Sept-Iles are similar for those arriving to Vancouver. Shipping patterns are similar in the two regions, in terms of vessel category (with ballast discharge coming from bulkers and tankers) and exchange method (flow-through is dominant) Lo et al. (in prep.). In addition, the North Atlantic and North Pacific have similar annual productivity of phytoplankton and macrozooplankton (Parsons and Lalli 1988).

Estimating effective propagule pressure involved a number of data corrections and assumptions. We assumed most data were accurately reported by ship officers and entered correctly into the database. Where obvious errors were detected, we corrected them when possible, such as when the wrong year had been inputted to the database, or when exchange dates were accidentally inputted as discharge dates. Where we encountered missing data (approximately 20% of the data), we made a number of assumptions (see Table 3.2). In particular, we assumed that the discharge volume is equivalent to the volume of ballast taken up in the source region, but only if vessel officers indicated the intent to discharge, and only if they did not provide a reason for not discharging ballast. In addition, where environmental data for a particular shipping port was not available from GloBallast, we used data available from the closest port.

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Table 3.2:Assumptions made to obtain parameter values for the model when components of data from the BWIS were missing (in total, approximately 20% of the entries). ER=empty-refill exchange, FT=flow-through exchange

Data Lacking	Assumed Values
Discharge Volume	Volume taken up at the source
Discharge Date	Arrival Date
Discharge Port	Arrival Port
Source Port	Last Port
% Tank Replacement for ER Exchange	Assumed 100% tank replacement
% Tank Replacement for FT Exchange	Assumed 300% tank replacement

Effect of mid-ocean exchange on final organism densities

We determined the effect of MOE on modeled total effective propagule pressure (N_t) by comparing N_t for exchanged and unexchanged tanks, for the species *E. acutifrons*, *P. parvus*, *M. edax*, and *D. mendotae*. To calculate final abundance in unexchanged tanks, the parameters μ_2 and 1- r_1 were removed from the model to result in the following equation:

Equation 3.5: *Final abundance in un-exchanged tanks*

$$N_{iD} = \sum_{j=1}^{Q} n_{ij0} v_j e^{-\mu_1 t_{sx}} r_2 \frac{1}{1+e^{-a(S_{sd}-0.5)}}$$

with t_{sd} representing time in days from source to discharge ports. We used our error values to obtain lower (N (low)) and higher (N (high)) estimates of abundance.

3.2.3. Effect of variation in mortality rates on final organism densities

We assessed how variation in mortality rates within tanks can affect the modeled abundances of ballast organisms. We obtained a range of initial mortality rates using randomly generated estimates of initial and final densities of an example species from our data set, *O. similis*, based on the sampling error (the coefficient of variation). We plotted the ratio of n_t, final density, when there is no mortality (i.e. μ_1=0) to n_t at varying values of μ_1.

3.2.4. Sensitivity analysis

We assessed the sensitivity of the similarity index, S_{sd}, to differently weighted temperature and salinity variables for twenty-five random voyages in our data set, across all three regions. We tested different weighting schemes by doubling and tripling the weight of temperature variables relative to salinity variables and vice versa. We also considered the effect of eliminating temperature or salinity variables from our calculation of S_{sd} on n_i. We determined the relationship between final densities, n_i (as in Equation 3.1), at differently weighted S_{sd}s to n_i with no manipulation of weightings (temperature and salinity variables weighted equally). For each weighting scheme, we recalculated all pairwise combinations of ports to recalibrate S_{sd}.

We test how changing S_{sd} from a sigmoidal to a linear, root, and power function affect the relative final modeled densities of organisms. We determined final organism density, n_{ijD}, as in Equation 3.1, with linear, logistic, root and power S_{sd} functions (described in the Appendix), holding the following constant: n_{ij0}= 46969.56, u_1=0.31, u_2=0.58, 1-r_1=0.1, r_2=0.99, t_{sx}=5 days and t_{xd}=5 days. We identified the strength of correlations between densities modeled with different S_{sd} functions, using Spearman's rank correlations. This statistical test was chosen to determine the strength of association between modeled densities, based on relative rankings of densities across voyages. We chose this test of sensitivity of relative densities because—given the parameter uncertainties—the predictions of the model are more appropriate in that forum than in the absolute densities of organisms.

Given our assumption of a sigmoidal relationship, we further test the sensitivity of modeled densities to various values of *a,* a constant that modifies the effect of environmental similarity and effectively changes the slope of the sigmoidal function (see Appendix for formula). We determined n_{ijD} at a =1, 25, 50, 75 and 100 across the same set of 25 voyages as above (and with the same constants), and determined the ratio of n_{ijD} with a=10 (our assumed value of a in our model) to n_t with a at various values (1, 25, 50, 75 and 100).

Statistical analyses were performed by using the Mann-Whitney test of central location, Spearman's rank correlation, and Pearson's correlation using S-Plus 8.0 (Insightful Corp. 2007) statistical software.

3.3. RESULTS

3.3.1. Daily mortality

The estimated mortality rate for species found on voyages bound for Sept-Îles and Hamilton are summarized in Table 3.3. Mortality rate and error calculations are shown in the Appendix.

Average daily mortality rates obtained from empirical data varied greatly between tanks. Assuming that there is no real variation in mortality rates, this likely reflects both sampling error and uptake of the target species during MOE.

The two calanoid initial mortality rates (μ_1) were similar (0.26 ± 0.01 for *A. clausii* and 0.28 ± 0.05 for *P. parvus*), although post-exchange, *P. parvus* had greater mortality (0.37± 0.02). The variation in cyclopoid mortality rates was higher, ranging from 0.03 ± 0.04 for *D. thomasi* to 0.35 ± 0.01 for *M. edax*.

Table 3.3: Initial, pre-exchange mortality rates (μ_1) and final, post-exchange mortality rates (μ_1) for zooplankton species on Atlantic and GLSL voyages, ± standard error, propagated from the sample coefficient of variation (Sept-Îles density data) and the reported sample standard deviations (Hamilton density data).

Atlantic[1*]					
Phylum	**Class**	**Order**	**Species**	μ_1	μ_2
Arthropoda	Copepoda	Calanoida	*Paracalanus parvus*	0.28 ± 0.05	0.37 ± 0.02
			Acartia clausii	0.26 ± 0.01	0.10 ± 0.11
		Cyclopoida	*Oithona minuta*	0.21 ± 0.32	0.17 ± 0.77
			Oithona similis	0.05 ± 0.06	0.25 ± 0.00
		Harpacticoida	*Euterpina acutifrons*	0.31 ± 0.07	0.58 ± 0.02
Great Lakes-St.Lawerence[2**]					
Arthropoda	Copepoda	Cyclopoida	*Mesocyclops edax*	0.35 ± 0.01	-0.24 ± 0.19
			Diacyclops thomasi	0.03 ± 0.04	0.17 ± 0.22
	Branchipoda	Cladocera	*Bosmina coregoni*	-0.11 ± 0.04	0.08 ± 0.16
			Daphnia mendotae	0.00 ± 0.01	0.53 ± 0.19
Rotifera	Monogononta	Ploima	*Polyarthra vulgaris*	0.31 ± 0.06	0.18 ± 0.29

[1*]Simard et al. *in press,* [2**]Gray et al. 2007

[*]Mortality rates obtained from average densities of two control and two exchanged tanks

[**] μ_1 was obtained by averaging 3 samples each for initial and final densities in the control tank; we solved for μ_2 given the parameters n_0, n_d, μ_1, r_1, t_{sx}, and t_{sd} in Eq. 1: $n_{ijD} = n_{ij0}\left(1-r_1\right)e^{-u_1 t_{sx}}e^{-u_2 t_{xd}}\,r_2\,\frac{1}{1+e^{-a\left(S_{sd}-0.5\right)}}$

3.3.2. Testing assumption of constant mortality

Our calculations of average daily mortality rates assume that mortality is constant through time. We tested this assumption of constant mortality by comparing CVs from the Atlantic voyage, which had no replicates of ballast water samples, to the CVs from the GLSL voyage, in which standard deviations attributed to sampling error could be determined from replicates. Significantly greater Atlantic CVs can thus mean that there was real variation in mortality rates that was not just attributed to sampling error, suggesting that mortality was not constant through time. We determined that the CVs from the Atlantic voyage (Sept-Iles to Rotterdam) were significantly greater than for the GLSL voyage (p=0.04), suggesting that there is significant variation in mortality rates with time on individual voyages. Using this test of our assumption involved another assumption – that differences in CVs were not just due to differences in abundance. To test this second assumption, we determined if the variation (standard deviation) was proportionate to the mean. We plotted CV and mean densities for GLSL species to test this assumption (Figure 3.1:

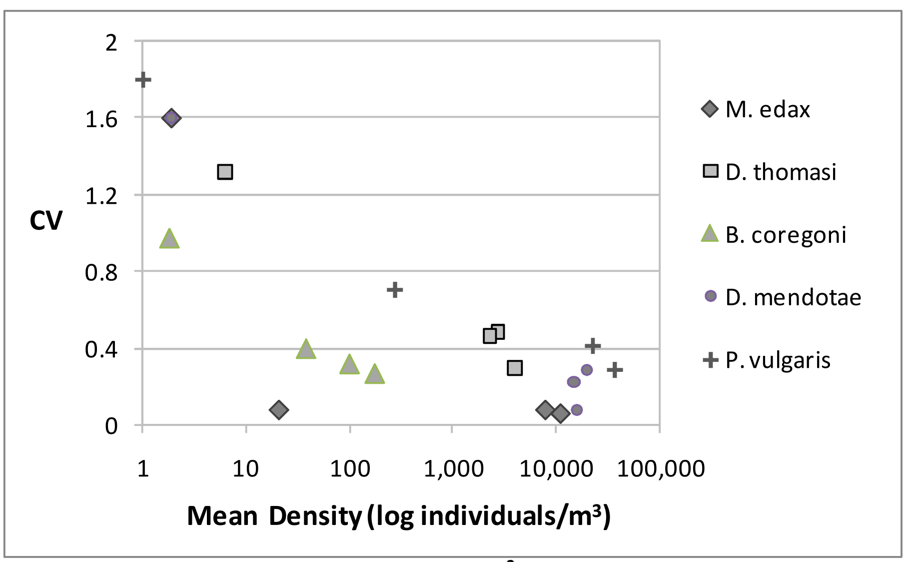

Figure 3.1: Final densities (log_{10} individuals/m^3) plotted against CV (coefficient of variation) for zooplankton species in the Great Lakes-St. Lawrence region

3.3.3. Effective propagule pressure

We used our model parameters (Table 3.1) in combination with shipping data to obtain estimates of annual effective propagule pressure of various ballast organisms (using Equation 3.2). Lower, mid and upper estimates, based on the propagated errors described above, are shown in Figure 3.2.

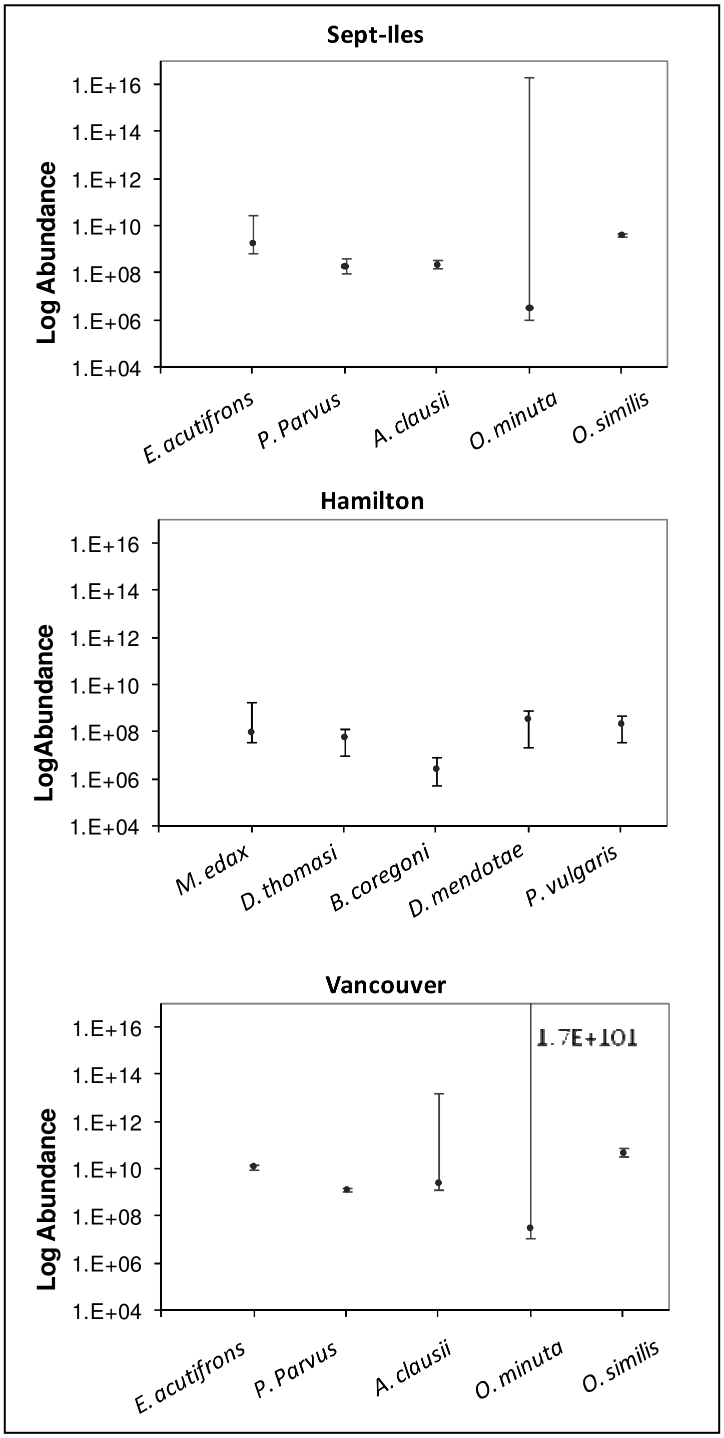

Figure 3.2: Modeled final abundance ($Log_{10}N_t$) (mid-estimates) of various zooplankton species discharged alive into Sept-Iles, Hamilton, and Vancouver. Mid-estimates are represented by circles, and low and high estimates are represented by dashes. Low and high estimates are the standard errors, obtained by calculations in Table A1.

3.3.4. Effect of mid-ocean exchange on final organism densities

Unexchanged ballast accounted for approximately 6%, 32% and 51.3% of the total ballast water volume discharged at Sept-Iles, Hamilton and Vancouver respectively, as reported in the BWIS (see Figure 3.3). Generally, this unexchanged ballast accounted for the majority of total abundances for Sept-Îles and Vancouver. However, up to 96% of the modeled total abundance of *M. edax* for Hamilton was attributed to exchanged ballast.

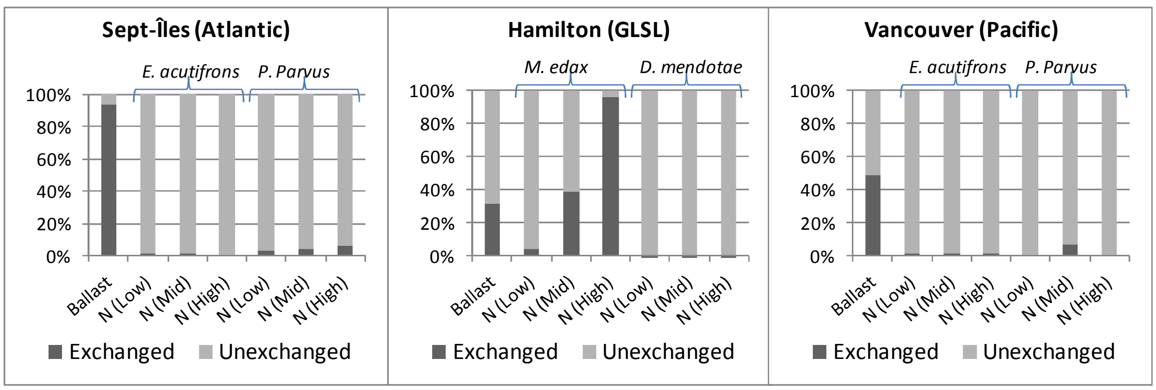

Figure 3.3: Percentage of effective propagule pressure attributed to exchanged and unexchanged ballast water discharged in the ports of Sept-Îles, Hamilton and Vancouver from October 1996-November 1997 for the species *E. acutifrons* and *P. parvus* (Sept-Îles and Pacific), and *M. edax* and *D. mendotae* (Hamilton). Final species abundances were modeled using high (N (Low)), mid (N (Mid)) and low (N (High)) mortality rates for a species. Unexchanged ballast accounted for the majority of effective propagule pressure in Sept-Îles and Vancouver. In Hamilton, exchanged water accounted for up to 96% of the total abundance of *Mesocyclops edax*.

3.3.5. Effect of variation in mortality rates

Results show that as t_{sx}, or time from ballast source uptake and exchange, increases, the final density (relative to no mortality) increases (See Figure 3.4).

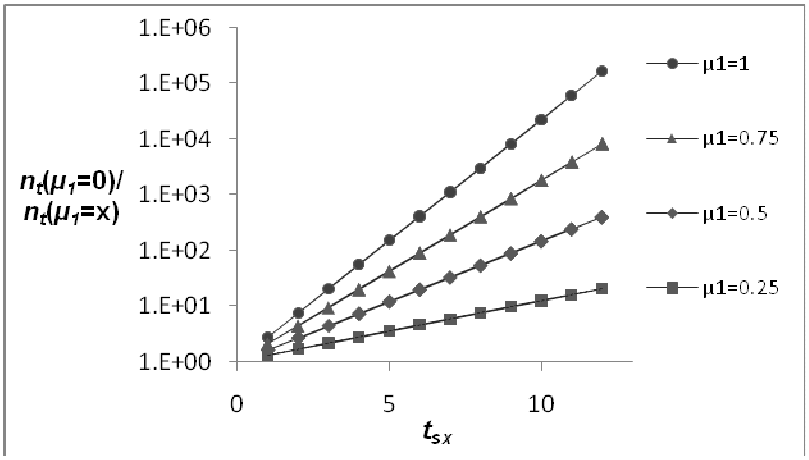

Figure 3.4: Time (t_{sx}: time from uptake to exchange in days) vs. relative final species density (n_t), measured as the ratio between n_t with no mortality (μ_1=0) and n_t with various mortality rates (μ_1=0.25, 0.5, 0.75, and 1).

3.3.6. Sensitivity analysis

3.3.6.1. Sensitivity to model to different temperature and salinity weightings in the environmental similarity index

Species densities were modeled with different weighting schemes for the environmental similarity index. We assume in our model that water temperature variables are equally weighted with salinity variables. We plotted different species densities over 25 representative voyages across the three shipping regions, using our assumed weighting scheme and six others. These were: inclusion of only salinity variables, and doubling and tripling the weight of salinity variables. We repeated these weighting schemes using water temperature variables (see Figure 3.5). Pearson's correlations on log abundances yielded high correlations between species densities with different weighting schemes (Pearson's *r* ranged from 0.96 to 0.99, p<0.001).

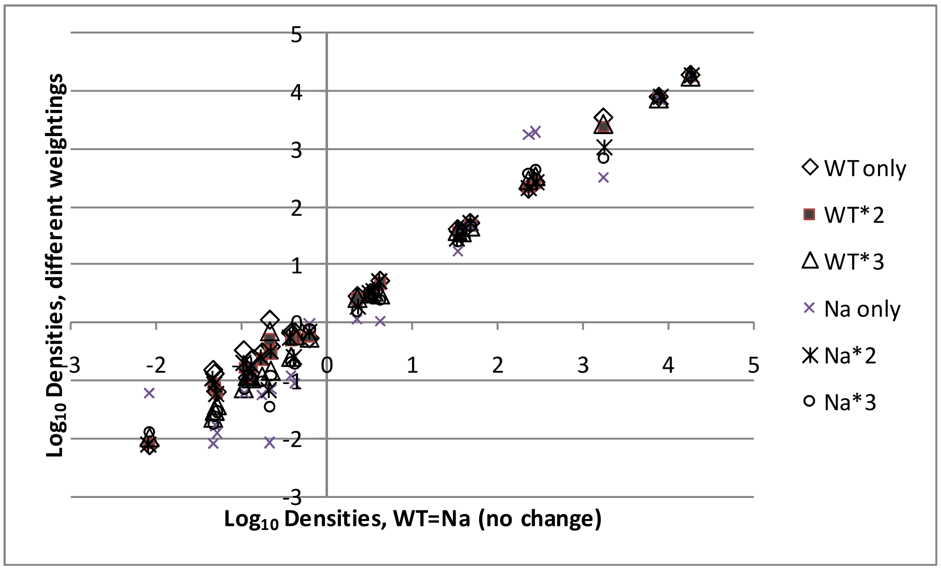

Figure 3.5: Sensitivity analysis: Log densities of species with different weighting schemes for the environmental variables in the similarity index vs. densities with no change in the weighting scheme. Weighting schemes are as follows: "T only" represents no consideration of salinity in S_{sd}, "T=3*Na" represents a temperature weighting of 3 times the salinity variables, and "T=2*Na" represents a temperature weighting of 2 times the salinity variables. "Na=2*T" represents a salinity weighting of 2 times the temperature variables, "Na=3*T" represents a salinity weighting of 3 times the temperature variables, and "Na only" represents no consideration of temperature variables in S_{sd}. On the x-axis, log densities were calculated with an environmental index where water temperature variables were weighted equally with salinity variables (WT=Na).

3.3.6.2. Sensitivity of model to different environmental similarity functions

Final densities for various species were modeled across a set of 25 voyages using four different S_{sd} functions. To avoid assumptions of normality, we use the Mann-Whitney U-test (or Wilcoxan rank-sum test) to test if final densities between groups have the same probability distributions. n_{ijD} using a power function for S_{sd} was significantly different from n_t using linear (p = 0.02), sigmoidal (p = 0.03) and root (p = 0.01) functions for S_{sd}. As expected, a Spearman's rank correlation test yielded significant correlations between the four groups (p<0.001 for all groups). The lowest correlations were between the power group with the linear (ρ = 0.88) and root (ρ = 0.80) groups. The highest correlations were between the linear and sigmoidal (ρ = 0.96) and linear and root (ρ = 0.98) groups.

3.3.6.3. Sensitivity of final densities to different values of a (1, 25, 50, 75 and 100)

Using our assumption of a sigmoidal function for S_{sd}, we modeled final densities across a set of 25 voyages, as above, using different values of the constant *a*, which modifies the steepness of the slope of the sigmoidal function. Pair-wise comparisons using the Mann-Whitney U-test yielded significant differences for n_t between the *a* = 1 and *a* = 100 pair (p=0.02).

3.6. DISCUSSION

3.4.1. Variation in mortality rates

We found major variation in effective propagule pressure between species. For the GLSL species *M. edax*, *D. thomasi*, *B. coregoni*, *D. mendotae* and *P. vulgaris*, the range from the low to high estimates of final abundances was on the scale of several orders of magnitude. For *O. minuta* abundance in the Pacific region, the scale ranged over 100 orders of magnitude. Mortality rates for these species are associated with larger errors than other species; all the GLSL had larger μ_2 (final mortality rate) errors than the Atlantic region species, with the exception of *O. minuta*, which had the largest error value of all the species considered in this model. *M. edax* had a negative mean μ_2, indicating apparent population growth and violating our assumption of no net reproduction. For *A. clausii*, *O. minuta*, *D. thomasi*, *B. coregoni*, and *P. vulgaris*, there was a large enough standard error in μ_2 that our confidence interval included the possibility of population growth.

We would expect mortality for zooplankton ballast water organisms to be higher after MOE, as the results of several studies reported lower post-MOE abundances (Gray et al. 2007; Wonham et al. 2005). However, calculated post-exchange mortality rates were lower than in the non-exchanged control tank for the copepod species *Acartia clausii* and *Oithona similis* (in the Atlantic voyage) and for the copepod *Mesocyclops edax*, cladoceran *Bosmina coregoni* and rotifer *Polyarthra vulgaris* (Great-Lakes voyage).

Possible reasons for apparent increases in abundance in the exchanged tanks (causing lower calculated mortality rates) are shifting ontogenetic stages from juvenile to adults, uptake of the species at the exchange site, and random sampling error. Lavoie et al. (1999) suggested that a developmental shift from younger to older stages was responsible for the increased abundance of copepod adults in exchanged tanks, as the increase in adult densities corresponded with decreases of copepod juveniles. However, the *A. clausii* and *O. similis nauplii*, or early larval stages, did not appear to have a decreasing trend. We could not obtain data on *M. edax* and *B. coregoni juveniles*, or *P. vulgaris* resting eggs. As *A. clausii* and *O. similis* are considered to be cosmopolitan species (Gubanova and Altukhov 2007; Takahashi and Ohno 1996), increased adult densities might be attributed to uptake at the exchange site. Similarly, *M. edax* is widespread in eastern and central North America (Allen 1984) and has been recorded in estuaries (Carter 1983), *B. coregoni* has been recorded in the Gulf of Finland (Põllumäe and Kotta 2007), and *P. vulgaris* has been observed at salinities from 0 to 39.1 parts per thousand throughout different seasons (Park and Marshall 2000). It is thus possible that these species can also tolerate salinities that they would likely be exposed to after MOE. Wonham et al. (2005) demonstrate through their model (also based on that of MacIsaac et al. (2002)) that under certain conditions MOE can result in increased densities of ballast organisms.

Lower post-exchange mortality rates (μ_2), or positive net population growth rates, as we saw in the above species, may also be a result of other components of mortality and population growth, which include physiological stress and starvation. MOE can reduce mortality and increase survival by bringing in nutrients, and/or removing predators/competitors. In a previous ship-board study by Gollasch et al. (2000), an increase in the abundance of the harpacticoid copepod *Tisbe graciloides* was observed, which may have been attributed to low competition through decreasing diversity, absence of predators and abundant food supply (Gollasch et al. 2000).

3.4.2. Variation in mortality rates within and between tanks and ships

There was considerable variation in mortality rates within tanks, reflected by the relatively large standard errors propagated from the original densities (Table 3.3). This variation caused calculated final abundances for the ports of Sept-Iles, Hamilton and Vancouver to vary by several orders of magnitude for some species (*O. minuta* (Sept-Îles), *E. acutifrons*, *P. parvus* and *A. clausii* (Vancouver), and *M. edax* and *O. similis* (Hamilton)) (Figure 3.2). Variation also changed the effect of MOE on final organism abundance. Our results showed that MOE can be ineffective depending on the value of the standard deviation of the mortality rate (Figure 3.3) – for Sept-Îles, a higher mortality rate resulted in the majority (83%) of the modeled effective propagule pressure arising from exchanged ballast water. For Hamilton, exchanged ballast water accounted for 100% of total effective propagule pressure using a lower estimate for the mortality rate. However, a study by Humphey et al. (2008) demonstrated that unexchanged ballast from vessels traveling intracoastally can have greater densities of zooplankton than exchanged ballast.

A 2000 study by McCollin et al. (2000) demonstrated significant inter-tank variability in the density and diversity of dinoflagellate cysts. A high degree of inter-tank variation has also been documented for dinoflagellate cyst abundances (Hamer et al*.* 2000). Similarly, Lavoie et al. (1999) and Smith et al. (1999) reported high variability in ballast organism densities between voyages. Thus, variation in mortality can exist within tanks, and across tanks, ships and voyages. Different sources of this variation are listed below:

Variation within ballast tanks:

- Experimental sampling error
- Variation across time within a voyage deriving from variation in abiotic conditions, prey items, predators, and competitors, all of which might stem from small variations in the populations taken up initially or during MOE

Variation across tanks:

- Tank position (e.g., aft peak, fore peak, side or double bottom): while ballast water temperature is primarily influenced by sea surface temperature, side tanks have been documented to vary in temperature more than fore or aft peak tanks, as they have greater exposure to the sun (Gollasch et al. 2000).
- Differences in tank construction can also influence the rate of sedimentation and thus organism concentration.
- Differences in other physical and abiotic factors causing increases in mortality: wave action in tanks, exposure to engine vibrations, availability of suitable settlement sites, physical injury during uptake, or toxic substances in ballast (Lavoie et al. 1999; Olenin et al. 2000). Abiotic conditions may vary greatly between tanks, a possible result of differences in tank construction, and consequently different components of the tank may concentrate ballast water from different source origins.
- Differences in biotic factors: predator-prey composition in the ballast water community, competition

- Variation in amount of ballast water taken up. However, Smith et al. (1999) reported that there was no significant relationship between plankton density and the amount of ballast water in cargo holds

Variation across ships:

- Differences in ship type (container, bulker, carrier, etc.), which may also be a reason for variation between and within tanks. However, a study by Choi et al. (2005) found that there was no significant difference in average zooplankton abundance in container ships and bulk carriers.

Variation across voyages:

- Exchange method: Different methods of MOE have different efficacies. Studies have shown that the ET (empty-refill) technique is more effective as a MOE technique than FT (flow-through) for typical tank volumes exchanged (Choi et al. 2005) or that variation in FT exchange is higher than in ET (McCollin et al. 2007; Ruiz et al. 2004)
- Seasonality: while Smith et al. (1999) found that the mean relative abundance of copepods was lowest in summer and highest in winter, more recent studies by Ruiz et al. (2007) found that exchange efficiency was not significantly different in voyages conducted in warm or cold temperatures.

3.4.3. Similarity index

There is a broad suite of environmental variables included in the IMO BWRA tool, including tidal range, rainfall, and air temperature, but we chose only the temperature and salinity variables for incorporation into a similarity index, for two reasons. First, temperature and salinity have been reported as parameters that most significantly affect abundances of copepods (Christou 1998), and including variables whose effect on invasion risk is unknown in an environmental similarity index may therefore dilute the risk of invasion (Barry et al. 2008). Tidal range will likely only impact survival of intertidal and littoral species, while rainfall and air temperature are unlikely to influence immediate survival of zooplankton species because changes in these variables will result in negligible changes to salinity and water temperature. One exception might be monsoon rains which may cause a decrease of salinity in an otherwise high salinity estuary.

Secondly, there are more data for temperature and salinity available for ports worldwide than there are for the other variables (BMT Fleet 2006). Temperature and salinity data can thus be verified with other sources, making these variables more reliable for a predictive model, while we must rely on a single, or few, estimates for the other parameters. Temperature and salinity tolerances differ by species, which we attempted to account for by using mortality rates derived from empirical ship-board abundances both pre- and post-MOE. By incorporating a similarity index, we can apply mortality rates to model abundances for other source ports. However, it is likely that weights of temperature and salinity on the similarity index should differ between species, and these different weightings can have significant effects on final abundances (Figure 3.5). There are also likely interactive effects of salinity and temperature tolerances on final abundances (Devreker et al. 2004), but we do not account for this possibility here due to a lack of data.

3.4.4. Data and model limitations and advantages

Applying this model to any given port requires identification of potentially invasive species, their survival in ballast water, and comprehensive data on shipping movements and ballasting activities. Such investigations can be time and cost-intensive, but can yield information on the effects of exchange on organism survival in addition to a rough estimate of expected effective propagule pressure. Caution must be employed when interpreting the results of our model, however, as our assumption of constant mortality may be incorrect, as evidenced by the significantly greater CVs for the Atlantic region.

A plot of CV and means for the species in the Great Lakes region (Figure 3.1) showed that our assumption of CVs being proportionate to the means is valid for species densities greater than 10 individuals m^{-3}. The plot also suggests that when organisms are at relatively low densities, the assumption that they are well mixed is false and that patchiness can be expected. At higher densities, it appears that species may be consistently well mixed, as CVs <1 imply relatively uniform spatial distributions.

A major limitation is the difficulty in accounting for all the sources of variation in abundance and mortality. In our study, an enormous amount of uncertainty stemmed from the variation in calculated mortality rates. As mentioned above, there are numerous reasons for variation, including local and regional, spatial, and temporal variation (Wonham et al. 2001).

Assuming that the model provides reasonable estimates of total effective propagule pressure, we probably underestimated propagule pressure for the three shipping ports, as some shipping data could not be included in the analysis because no ballast uptake source dates were given (approximately 20% of the entries in the database).

Additionally, this model is appropriate for an estimate of effective propagule pressure of ballast water organisms, but not of ballast sediments. Recent studies (e.g. Bailey et al. 2005; Gray et al. 2005) have investigated the potential for invertebrate diapausing eggs in sediments to survive mid-ocean exchange and hatch after being discharged to a port. The effect of exchange on egg survival will likely be modeled in a different manner than presented above, as eggs are more tolerant to changes in salinity. Gray et al. (2007) found that the total abundance and species richness of hatched invertebrates was not affected by exposure to saline (32 parts per thousand) water. Similarly, this model does not account for organisms transferred by hull fouling (as described in Minchin and Gollasch 2003), which will be more important for ports that receive a high number of arrivals relative to the total amount of ballast water discharged, such as the port of Victoria on the Pacific coast, which receives traffic principally from cruise ships with relatively lower volumes of ballast water.

However, we have been able to account for a number of assumptions that have been made for previous estimates of propagule pressure. Barry and Levings' (2002) assumed that survival during uptake, transit and discharge was 100% for their population model of the copepod *Pseudodiaptomus marinus*, while MacIsaac et al. (2002) obtained mortality rates in exchanged tanks for Great Lakes voyages by assuming that the total survival of organisms over a five-day journey is two orders of magnitude lower in saltwater (after exchange) than in freshwater. Various ship-board studies such as Grey et al. (2007) demonstrate that survival is likely not constant for all species for each stage of a voyage, and that the ratio between survival pre- and post-exchange varies, illustrating the error in making such assumptions. Our model also incorporates uncertainty estimates to ensure conservatism in our results.

3.7. CONCLUSION

We used a novel approach to quantify effective propagule pressure for shipping ports, using comprehensive shipping data in addition to empirically-derived mortality rates and source-discharge environmental similarity.

Variation in mortality rates due to sampling error of initial and final organism densities may yield high variation in modeled final abundances, and may theoretically determine whether MOE is effective in reducing effective propagule pressure for certain ports or species. 94% of the ballast water discharged at Sept-Iles between November 2006 and

October 2007 was reported as exchanged, and one might assume most AIS were removed via MOE. However, over 90% of the modeled total final abundance of *E. acutifrons* (N (High)) came from the exchanged ballast water. All of the modeled abundance (N (low)) of *O. similis* came from exchanged ballast water as well (see Figure 3.3).

Our analysis indicates that our model of effective propagule pressure was not sensitive to different weighting schmes, for the 25 voyages we tested (Pearson's ranged from 0.96 to 0.99, $p<0.001$).

Different functions for the environmental similarity index, and different coefficients within a given function, yielded significantly different final organism densities. Results using a power function for the environmental similarity index were significantly different from linear, sigmoidal and root functions ($p<0.05$). However, modeled densities were not sensitive to changing environmental similarity functions across the same set of 25 voyages tested above (Spearman's ρ ranged from 0.8 – 0.98, $p<0.001$).

This model was used to calculate total abundance of a target species introduced to shipping ports over a one-year period. Given comprehensive shipping data, we can quantify abundances of a target species for multiple ports in a particular region. This would allow identification of the ports that are more likely to receive greater effective propagule pressure, such as areas receiving coastal unexchanged ballast water, and consequently are best to target for management actions.

As the precise relationship between propagule supply and risk of establishment, or realized propagule pressure, has not yet been clearly determined (Ruiz et al. 2007), this study can also be a starting point in determining this relationship by characterizing effective propagule pressure for Canadian shipping ports. Further studies exploring the variation of mortality across ships, time and space, and on how various ballast organisms respond to salinity and temperature tolerances, will improve future attempts to predict effective propagule pressure.

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4. CONCLUSION

4.1. STATUS OF CURRENT RESEARCH ON PROPAGULE PRESSURE OF AQUATIC INVASIVE SPECIES

4.1.1. Linking invasiveness, invasibility and propagule pressure

Factors controlling establishment success of invasive species include species-specific characteristics (invasiveness), ecosystem characteristics (invasibility), and propagule pressure, as discussed in Chapter One. There have been few attempts to thread together these diverse factors into a comprehensive picture of invasion risk. However, Leung et al. (2007) and Herborg et al. (2007) created models of invasion risk that incorporate both invasibility and propagule pressure. The model developed by MacIsaac et al. (2002) and adapted by Wonham et al. (2005) incorporates propagule pressure and species-specific mortality rates. We further developed this latter model, described in Chapter Three, by including an index reflecting the environmental similarity of source and discharge ports. The model predictions thus include components of propagule pressure, invasibility and species-specific characteristics.

4.1.2. Progress in determining propagule pressure

Propagule pressure is an emerging area of study, but there has been a greater focus on terrestrial ecosystems as data are easier to collect, monitor and manipulate than for aquatic ecosystems (i.e. Rouget and Richardson 2003). Despite these limitations, progress has been made in characterizing propagule pressure of ballast water organisms. Ruiz and Reid (2007) have synthesized some of the literature on ballast water effectiveness. Work remains, though, on characterizing the risk of diapausing eggs in the sediments of ballast tanks (Bailey et al. 2004), risks posed by fouling organisms (Frey et al. 2009), as well as viruses and bacteria in ballast water (Drake et al. 2002).

4.1.3. Assessing risk of invasive species introductions

Risk assessments of species introductions via ballast water are generally conducted by using species-specific or environmental similarity approaches (Barry et al. 2008). Species-specific approaches use information on life history and physiological tolerances to inform survival rates. The model described in Chapter 3 does not calibrate survival functions for individual species, although this function likely varies across species. Another drawback is the amount of data required to perform such risk analyses, which may include life history and physiological tolerance data at each life stage, species presence or absence information, as well as behavioural, reproductive, and predation characteristics (Barry et al. 2008). The availability of these data may restrict such risk analyses.

Environmental similarity approaches, while unencumbered by these data requirements, do not account for differences between species in their response to different environmental conditions. This approach also requires careful selection of environmental variables to ensure the sensitivity of the environmental similarity measure - in our case, an index of environmental similarity between source and discharge ports (Barry et al. 2008). In Chapter Three, I have used a quantitative approach to risk assessment, integrating both the species-specific and environmental similarity approaches into one model.

4.2. WEAKNESSES AND STRENGTHS OF THESIS RESEARCH

4.2.1. Weaknesses

Determining potential and effective propagule pressure of AIS using the methods outlined in this Chapters Two and Three in this thesis required extensive data on ballast discharge locations.

The submission of ballast reporting forms are now mandatory in Canada under ballast management regulations, but are voluntary in other countries. Even with the availability of ballast data, staff and monetary resources are required to manage and transfer the forms to the database in an efficient, accurate and timely manner. In Canada, it has been a challenge to government staff to ensure that ballast water reporting forms were collected, entered, and verified, and also a challenge to store the data in an accessible yet confidential way. Because of this, it took several attempts and staff time to obtain a relatively complete set of data. Estimating propagule pressure with the methods described in this thesis, therefore, will be more of a challenge in resource-poor areas with little capacity to conduct this work.

While the focus of this thesis is mainly on AIS introduced via ballast water, I investigated the potential propagule pressure of hull fouling organisms in Chapter Two. Because the data set I used was limited to commercial vessels discharging ballast, many smaller vessels that do not typically discharge ballast, such as recreational boats, were not included in the analysis. The strength of the hull fouling vector was likely underestimated as a result.

For the model we present in Chapter Three, port environmental conditions and species-specific mortality rates are required in addition to the above data. Environmental data were obtained from the International Maritime Organization Ballast Water Reporting

Tool. These data were gathered from numerous sources, including scientific, government and port publications, web sites, sampling records, survey reports, SST charts, salinity charts, climate databases, atlases, national tide-tables, nautical charts, coastal habitat maps, national habitat databases, OSCPs, aerial photographs and local expert advice (International Maritime Organization 2006). Consequently, the data may not be standardized for all ports. Additionally, ballast is not always taken up at the departure port, but it is difficult to obtain environmental data for all locations where ballast is taken up. Nonetheless, these environmental data are probably the best available on a global scale.

Species-specific mortality rates are a large data obstacle, as the availability of data depends on empirical studies. While there are several investigations of ballast water effectiveness, these studies usually measure abundances post-exchange (Choi et al. 2005), or after ballast is taken up and before exchanged ballast is discharged (Verling et al. 2005). For the model I used, abundances are required immediately after exchange and before discharge, in order to obtain post-exchange mortality rates. I applied mortality rates obtained from a few voyages to all the voyages in the data set for a given region, as we lacked empirical data to inform species mortalities under different voyage conditions. In order to estimate effective propagule pressure, I thus had to assume that the calculated mortality rates were similar for all voyages in a particular region, effectively assuming there were no differences in mortality rates across seasons and ocean environments for all the voyages we considered. The lack of availability of mortality data on invasive species also meant that I had to parameterize the model using species that are not known to be invasive in Canadian waters.

By applying the empirically-derived average daily mortality rates from a few voyages to all the voyages in our data set, we assumed that different environmental conditions on these voyages would not affect mortality. In reality, it is likely that that voyage conditions will significantly alter mortality. Another weakness is our assumption that mortality rates are the same for all life history stages of a particular species; for example, the differences between adult and juvenile life stages are not accounted for. A population age-stage model (i.e. Hu et al. 2008) would generate more accurate predictions of surviving species abundances.

4.2.2. Strengths

Chapter Two of this thesis is the first comprehensive national investigation of ballast water discharges in Canada since the federal ballast water regulations came into force in 2006. This analysis was drawn from a comprehensive national database, and is the first study quantifying potential propagule pressure of hull fouling and ballast water species from the commercial shipping sector. The timeframe for our shipping data was selected for after the federal ballast water regulations came into force in 2006, meaning that more accurate quantifications of potential propagule pressure could be conducted since it became mandatory to report ballast discharge. The shipping profile provides a first-pass identification of ports that have the highest potential for AIS establishment from both ballast and hull fouling species. A globally novel aspect of this shipping profile is my attempt to determine relationships between various proxies of propagule pressure. My analysis shows that arrivals are significantly correlated with both ballast and wetted surface across shipping ports, but the degree of correlation varies by shipping region. As data on arrivals are easier to obtain than data on both ballast discharge and wetted surface area, this means that for certain shipping regions, arrivals could be an adequate indicator of propagule pressure when more precise estimates are difficult to make due to lack of data.

In Chapter Three, I adapted the model by MacIsaac et al. (2002) to the prediction of effective propagule pressure by incorporating an environmental similarity index and parameterizing it with comprehensive Canadian ballast water data. I thus employed a combination of a species-specific and environmental similarity approach to estimating risk of ballast water invasion, in addition to combining components of invasiveness (species-specific mortality rates), and propagule pressure (quantitative model of organism abundances). By using empirical data to inform mortality rates, we avoided the assumptions made previously by MacIsaac et al. (2002) that mortality rates are similar for species within broad taxonomic groups (e.g. copepods and rotifers). We were also able to calculate post-exchange mortality rates from empirical data, avoiding using general blanket assumptions, such as MacIsaac et al.'s assumption in their model that that the 5-day survival rate of organisms is two orders of magnitude lower than survival in fresh water.

Additionally, the quantitative model accounts for the effect of ballast exchange on organism survival, unlike some risk assessment tools, such as the Ballast Water Risk Assessment Tool developed for the international GloBallast Programme, which calculates the relative risk of a port to ballast-mediated introductions of AIS (International Maritime Organization 2006). Accounting for the proportion of ballast exchanged is another important improvement over MacIsaac et al.'s (2002) model, as they assumed that all vessels undergo nearly complete exchange.

This model showed that much variation exists for total mortality across the voyage, probably a result of variation in voyage conditions. It is evident that the effectiveness of MOE can depend on the magnitude and direction of this variation. These results highlight the importance of uncertainty and variability in ballast water risk assessments for Canada.

4.3. SIGNIFICANCE OF RESEARCH FINDINGS

I have investigated the potential propagule pressure of AIS to Canadian shipping ports by estimating the strength of the ballast water vector. I identified shipping ports where potential propagule pressure is likely highest, and thus where management efforts might be best directed. I took these potential propagule pressure estimates a step further by modeling species abundances after ballast discharge, incorporating species-specific survival rates and the environmental similarity between the source and discharge points, in addition to accounting for the effects of ballast water exchange on organism survival. While these estimates of propagule pressure do not account for the likelihood of establishment success, the characterization of potential propagule pressure allows for the separate testing of the various stages of introduction, which is an important advancement in invasion ecology.

4.4. FUTURE RESEARCH DIRECTIONS

As the risk of introduction of AIS will depend on the life stage of a particular species, it will be important for future risk assessment models to account for differences in life stages. Diapausing, or 'resting' eggs are produced by many zooplankton, including copepods, cladocerans and rotifers (Bailey et al. 2004). These resting eggs may protect against unfavourable environmental conditions, such as anoxia and changes in temperature and salinity (Bailey et al. 2004). Ballast tanks, particularly in vessels with NOBOB status, can contain hundreds of thousands of viable invertebrate diapausing eggs (Duggan et al. 2005). Diapausing eggs may be released into the environment as live individuals after hatching in ballast tanks, or directly released when residual sediments are disturbed during ballast discharge (Bailey 2005). Wonham et al. (2005) modeled the invasion risk of diapausing organisms, but did not consider in the model the tolerance of certain species to differences in environmental conditions. A critical component of future modeling efforts will be determining how mortality varies with environmental conditions throughout the voyage in addition to source and destination ports.

The approaches to estimating propagule pressure presented in this thesis are specific to organisms introduced by ballast water. However, hull fouling is also increasingly being recognized as an important vector of propagule pressure of AIS (e.g. Drake and Lodge 2007; Mineur et al. 2008). Incorporating this vector into estimates of propagule pressure resulting from shipping activities will be an important future research effort. These efforts will likely need to account for fouling (particularly areas on the hull such as rudder faces, propellers, and sea chest grates), the use of anti-fouling paints, vessel cleaning history, and differences in environmental conditions that organisms will encounter throughout the entire journey.

The largely unregulated aquarium and ornamentals trade is an emerging vector of concern (Padilla and Williams 2004). In addition to increased propagule pressure from these sources, the effects of climate change will expand introduction pathways of new species, for example, via increased flooding events and new opportunities for aquaculture facilities for warm water species (Rahel and Olden 2008). The establishment success of many introduced species will likely increase as water temperatures warm and as streamflow regimes and salinity levels of aquatic ecosystems are altered (Rahel and Olden 2008). Given that the increasing number of AIS introduction pathways in addition to shipping activities, and the harmful consequences of AIS establishment, further research in invasion ecology is needed to understand how establishment success is related to propagule pressure. My novel method of characterizing propagule pressure, using comprehensive shipping data and mechanistic models of organismal transport and survival, provides a good start for understanding this relationship.

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APPENDIX

CHAPTER TWO

Wetted Surface Area, as calculated by Davidson et al. (2007), using methods by Van Maanen & Van Oossanen, 1988:

WSA= L (2T + B) C_M0.5 (0.4530 + 0.4425 C_B - 0.2862C_M – 0.003467B/T + 0.3696 C_{WP}) + 2.38A_{BT}/ C_B
where: L = length, T = draft, B = breadth, C_M = midship coefficient, C_B = blocking coefficient, C_{WP} = waterplane coefficient, A_{BT} = cross-sectional area of bulbous bow (calculated as a percentage of the immersed area of midship).

CHAPTER THREE

Euclidean Distance, ED

The Euclidean distance, *ED*, is the "ordinary" distance between two points that one would measure with a ruler, which can be proven by repeated application of the Pythagorean theorem. The Euclidean distance in environmental conditions between source port *s* with environmental variables $s_1, s_2 \ldots s_n$, and discharge port *d* with environmental variables ($d_1, d_2 \ldots d_n$), in Euclidean *2*-space, is the following:

$$ED = \sqrt{\sum_{i=1}^{n} (s_i - d_i)^2}$$

ED values were calculated between ports *s* and *d* with standardized environmental variables. For a particular environmental variable, *v,* we calculated its standardized value, v_s, by the following formula:

$$v_s = \frac{v - \mu_v}{\sigma_v};$$

where μ_v is the mean and σ_v is the standard deviation of *v* across 599 international shipping ports

Environmental Similarity Index, S_{sd}

Values for the environmental similarity index between source (*s*) and discharge (*d*) ports, S_{sd}, were calculated by the following formula:

$$S_{sd} = \frac{|(ED - ED_{\max})|}{ED_{\max}};$$

where ED is the Euclidean distance between ports *s* and *d,* and ED_{max} is the *ED* value between the source port and the maximally different destination port

Exchange Efficiency for Flow-Through Mid-Ocean Exchange

(Modified from Rigby and Hallegraeff (2004))

$$E = 100 - ae^{-bx};$$

where *E* is the exchange efficiency for flow-through MOE, *x* represents percent tank replacement by MOE, and *a* and *b* are constants with values of 100.1 and 0.01, respectively (see Figure A1).

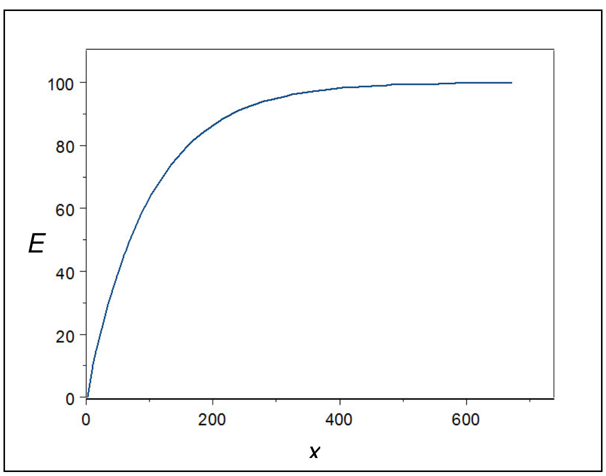

Figure A1: A function for exchange efficiency for flow-through MOE. *E*=exchange effiency for flow-through MOE, and *x*=percent tank replacement.

The probability of an organism being discharged during MOE, r_1, can thus be calculated using the formula $r_1 = 1 - \frac{E}{100}$.

Calculation of CV (coefficient of variation)

$CV = \frac{\sigma}{\mu}$; where σ = standard deviation and μ =mean of final densities over time within a tank and within a voyage.

$\sigma = \frac{\sqrt{S}}{n-1}$;

Where *S* = sum of squared errors between predicted final densities (assuming constant mortality across time) and actual final densities and *n* = number of observations (of abundance).

Mortality Rates and Uncertainty

Formulas for the model parameters and error calculations are given in Table A1. Based on the propagation methods described in Taylor (1997) (Table A2), we calculated error values for pre-exchange mortality (μ_1) and post-exchange mortality (μ_2). t_0, t_x and t_d represent the time in days at ballast uptake, exchange, and discharge; n_o, n_d and n_x are species densities after ballast uptake, just after exchange, and at the point of ballast discharge; and *CV* is the coefficient of variation (ratio of the standard deviation to the mean).

Table A1: Formulae for mortality rates and uncertainty calculations

Region	Formula	Calculation of Uncertainty (*u*)
Atlantic	$\mu_1 = \frac{-\ln(n_d/n_0)}{t_d - t_0}$	$u\{\mu_1\} = \frac{CV \cdot \sqrt{2}}{(t_d - t_0)}$
	$\mu_2 = \frac{-\ln(n_d/n_x)}{t_d - t_x}$	$u\{\mu_2\} = \frac{CV \cdot \sqrt{2}}{(t_d - t_x)}$
Great Lakes-St. Lawrence	$\mu_1 = \frac{-\ln(n_d/n_0)}{t_d - t_0}$	$u\{\mu_1\} = \frac{\sqrt{\left(\frac{u\{n_d\}}{n_d}\right)^2 + \left(\frac{u\{n_0\}}{n_0}\right)^2}}{(t_d - t_0)}$

For the Great Lakes-St. Lawrence region, we solved for μ_2 using a modified version of Equation 3.1:

$$n_{ijD} = n_{ij0}(1 - r_1)e^{-u_1 t_{sx}} e^{-u_2 t_{xd}} r_2 \frac{1}{1 + e^{-a(S_{sd} - 0.5)}}$$

As we are interested in the mortality rate after exchange but prior to discharge, we eliminated the terms r_2, the probability of discharge while the ship discharges ballast, and S_{sd}, the similarity term:

$$n_{ijD} = n_{ij0}(1 - r_1)e^{-u_1 t_{sx}} e^{-u_2 t_{xd}}$$

Solving for μ_2:

$$\mu_2 = \frac{-\ln\left(\frac{n_t}{n_0(1 - r_1)}\right) - \mu_1 \cdot t_{sx}}{t_{xd}}$$

The associated error of μ_2 is:

$$u\{\mu_2\} = \frac{1}{t_{xd}} \sqrt{\left(\sqrt{\left(\frac{u\{n_t\}}{n_t}\right)^2 + \left(\frac{u\{n_0\}}{n_0}\right)^2}\right)^2 + (t_{sx} \cdot u\{\mu_1\})^2}$$

Table A2: Propagation of Errors, modified from Taylor 1997

Operation	Example	Uncertainty Calculation
Addition/Subtraction	$x = a + b$	$u\{x\} = \sqrt{(u\{a\})^2 + (u\{b\})^2}$
Multiplication/Division	$x = a \cdot b$, $x = a/b$	$u\{x\} = x\sqrt{\left(\frac{u\{a\}}{a}\right)^2 + \left(\frac{u\{b\}}{b}\right)^2}$
Multiplication by a constant, *k*	$x = k \cdot a$	$u\{x\} = \lvert k \rvert \cdot u\{a\}$
Logarithm	$x = \ln a$	$u\{x\} = \left\lvert \frac{u\{a\}}{a} \right\rvert$

Relationship between Survival upon discharge, S, and Environmental Similarity, S_{sd}

Function	Formula
Logistic	$S = \frac{1}{1 + e^{-10(S_{sd} - 0.5)}}$
Root	$S = \sqrt[3]{S_{sd}}$
Power	$S = (S_{sd})^3$