Optimizing monitoring and eradication of invasive species:
new frameworks and applications

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Preface

Thesis Format and Style

This thesis is in a manuscript-based format and consists of a set of four papers that make a cohesive whole.


Contributions of co-authors

The preparation of each of my thesis chapters was helped substantially by the co-authors on each of the individual manuscripts. The primary role in each was always my own, but I am grateful for their contributions. I detail the specific contributions of my co-authors to each chapter here.

Chapter 1: In this and the following chapter S. Collin (under the guidance of L. Johnson) gathered the biological data necessary for the analysis. Both S. Collin and L. Johnson provided comments during the preparation of the manuscript and discussion on the ideas presented. B. Leung, in addition to commenting on the manuscript, assisted in the conception of the idea of this manuscript and its technical execution. I further developed the ideas in this chapter, wrote the manuscript and did all analysis.

Chapter 2: L. Johnson, B. Leung and S. Collin had identical contributions to this chapter as they did in Chapter 1. Additionally, T. Guyondet provided manuscript comments, finalized a hydrodynamic model initiated by G. Seibert and provided the output velocity fields from it, and a copy of a piece of software (written by M. Foreman and others) to move particles within the fields. I was able to modify this software and employ it to simulate larval dispersal for this study. B. Leung and L.
Johnson helped conceive of the idea for this chapter and provided comments on
the manuscript. I further developed the ideas of this chapter, wrote the
manuscript and performed all analysis.

Chapter 3: In this chapter B. Leung helped conceive the idea and provided
comments during my preparation of the manuscript. I further developed the ideas
and prepared the manuscript.

Chapter 4: G. Ruiz and L. Johnson provided helpful discussion on the type of
data collected and the methodology to collect it. In addition, G. Ruiz availed of
me the resources of the Smithsonian Environmental Research Center, including
lab space and field assistants. He also provided comments on the final version of
the manuscript. B. Leung helped conceive the idea for the chapter and provided
comments during my preparation of the manuscript. I further developed the ideas
for this chapter, prepared the manuscript, performed field work, and did all
analysis.
Original contributions to knowledge

Chapter 1 examines how to detect invaders, prior to beginning an eradication program. The chapter adds to the field of species distribution models by developing a new type of this kind of model that combines dispersal and environmental tolerance. It is the first to demonstrate how this model (and others like it) can be used to capture the mechanics of larval dispersal and to design monitoring programs to detect larvae of invading species.

Chapter 2 demonstrates how models like that in Chapter 1 can be used as alternative models against which more advanced physical models can be compared. In certain cases these simpler statistical models may be highly effective and may preclude the costly development of physical models. This paper also presents a framework for the comparison of arbitrary dispersal models, despite possible incompatibilities in their outputs. The chapter demonstrates how this framework can be used to compare statistical and mechanistic models of dispersal.

Chapter 3 offers the first ever quantitative framework for eradication of invasive species. Following detection of an invader (e.g., with methods from Chapter 1 or 2) this chapter offers managers equations and tools to determine the cost, scope,
timing, and overall feasibility of an eradication program, and suggests the necessary data to collect to reach these conclusions.

Chapter 4 extends the first chapter. It draws upon Chapter 3 and other published eradication frameworks to create a review of the 43 criteria suggested for eradication. It distills the key elements from each and fills gaps in their advice, and removes redundant or contradictory advice to create decision tree for eradication – a more complete eradication framework. It is a timely review of published eradication guidelines, and the most general and quantitative eradication framework available to date.
Thesis abstract

This thesis develops new statistical, and decision making tools for the detection and eradication of invasive species. The first section develops models to predict locations of invasive species so monitoring effort can be concentrated there. The first chapter develops an advanced species distribution model that includes dispersal and environmental tolerances and outperforms traditional species distribution models of just environmental tolerances. In addition this model is able to capture estimates of the target species fecundity, dispersal range, environmental tolerances and conspecific larval aggregation. The second chapter compares the performance of this statistical model to a popular form of mechanistic hydrodynamic model that is widely used to model dispersal, but which is rarely validated. By comparing the two approaches I show how advanced species distribution models can be used as alternative models to assess the power of more expensive, computationally demanding mechanistic models and how in some cases the statistical models may perform as well for a fraction the cost.

The second section of my thesis examines how to formulate a response to an invasion once it is detected. The first chapter develops the first quantitative framework for eradication. It suggests that eradication can proceed without
directly targeting all life stages and the number of treatment passes and their timing can be calculated from basic biological data like maturation rates. The final chapter incorporates guidance from other published eradication frameworks. It modifies and amends them to form a decision tree of necessary experiments to determine eradication feasibility and timing. It adds to the previous chapter explicit consideration of mobility, immigration, and spatio-temporal variation in vulnerability to form a more complete eradication framework.
Résumé

Cette thèse développe de nouveaux outils statistiques qui peuvent être utilisés dans les prises de décision afin de détecter et d’éradiquer les espèces invasives. La première section de la thèse développe des modèles permettant de prévoir la localisation des espèces invasives afin d’identifier les lieux où les efforts de surveillance devenaient être concentrés. Le premier chapitre développe un modèle de distributions d’espèces qui incluent les tolérances environnementales et la dispersion et ce faisant performe mieux que les modèles traditionnels qui n’incluent que les tolérances environnementales. De plus, ce modèle peut estimer des paramètres clés d’espèces cibles, comme la fécondité, le potentiel de dispersion, la tolérance environnementale et l’agrégation des larves de conspécifiques. Le deuxième chapitre compare la performance du modèle statistique du premier chapitre à un modèle mécanistique hydrodynamique grandement utilisé en modélisation de dispersion, mais, en revanche, qui est rarement valider. En comparant les deux approches, je démontre comment les modèles de distributions d’espèces peuvent être utilisés comme modèles alternatifs pour évaluer le pouvoir de modèles mécanistique plus coûteux et informatiquement demandant et comment, dans certain cas, les modèles statistiques peuvent performer aussi bien mais pour une fraction des coûts.
La deuxième partie de ma thèse examine comment formuler une stratégie d’intervention à une invasion quand cette dernière est détectée. Le premier chapitre développe une approche quantitative pour évaluer les éradications, une première de cette envergure. Elle suggère que les éradications peuvent se dérouler sans directement cibler tous les stages de vies, et le nombre de traitements ainsi que leur intervalle d’application peuvent être calculés de données basiques biologiques, comme les taux de maturations. Le dernier chapitre incorpore les considérations des autres schémas d’éradications publiés dans la littérature. La méthode modifie et amende des schémas publiés en formant un arbre de décisions d’expériences nécessaires qui ensuite détermine la faisabilité et l’envergure de l’éradication. Ce chapitre ajoute aux chapitres précédents, considérant explicitement la mobilité, l’immigration et la variation spatio-temporelle de la vulnérabilité, pour produire une approche compréhensive des schémas des réponses aux éradications.
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General Introduction

Accelerated international transport has allowed the easy movement of people, goods and ideas around the world. This transport has also facilitated the movement of species across oceanic and continental divides that had limited their movement for millions of years. Varyingly called “non-indigenous,” “alien,” “exotic,” or “invasive” species are those that are imported by humans across a major geographic barrier, and survive in their new environment where they spread and cause harm (Richardson et al. 2000, Lodge and Shrader-Frechette 2003). They occur on land, in forests, tundra, and jungle, they can be found in oceans, lakes, stream, and estuaries and on every continent (Strong et al. 2008), including Antarctica (Smith et al. 2012).

Aquatic Invasive Species (AIS) threaten coastal diversity and commerce worldwide (Carlton 1993, Mack et al. 2000, Ruiz et al. 2000b, Occhipinti-Ambrogi and Savini 2003). AIS can impact the recipient community in many ways: they can out-compete local species for resources (e.g., food, space), alter local environments (Cuddington and Hastings 2004), and carry harmful pathogens (Ruiz et al. 2000a, Minchin 2007). Additionally, AIS can impact commercially valuable species, where economic costs can reach billions of dollars (Pimentel et al. 2005). Due to the ecological damage they cause, invasive species are
considered the second greatest cause of biodiversity loss worldwide (Wilcove et al. 1998).

The increasing rate of global introductions (Ruiz et al. 2000b) and the ecological and economic damages they cause compel us to devise management action that can reduce, if not prevent, the impact of AIS on local communities and industries. One of the tenets of AIS management is that, on balance, earlier action is more effective than later action and a management effort is more likely to succeed when population are detected early and controlled before they spread significantly (Myers et al. 2000). Early detection, coupled with effective control (like rapid response protocols that include evaluation of eradication), can slow the spread (Sharov and Liebhold 1998) and reduce, if not entirely negate the impacts of even the most problematic AIS (Naylor 2000, Brooks et al. 2004).

Regrettably, much monitoring for invasive species is done haphazardly, rather than being guided by ecological tools and this is a field where quantitative frameworks are useful and needed (Fox et al. 2009). Most AIS follow a common reproductive method whereby adults release gametes or larvae directly into the water (Gaines and Bertness 1992) and monitoring can be conducted by searching for any of these stages. Monitoring for AIS in marine systems usually
consists of active searching by SCUBA teams to find adults, or less commonly by
stations to detect their larvae (Campbell et al. 2007). This type of larval
monitoring is done by genetic probes (Lodge et al. 2012) or with plastic plates
that encourage recruitment of larvae (e.g., Lacoursière-Roussel et al. 2012,
Collin et al. in press).

Because of the mixing nature of marine systems, these released larvae are
usually more numerous and distributed much wider than were the adults which
released them (Kraft and Johnson 2000). Therefore, monitoring for the larvae of
a target invader can yield more detection events in more areas than looking
directly for adults, potentially leading to more fruitful monitoring programs.

Recruitment of marine organisms is known to be influenced by environmental
factors and predictive models of recruitment are applied to forecast stocks of
commercial species based on environmental properties (e.g., Daskalov 1999),
but fewer predictive models of larval abundance are available. I concentrate the
first section of my thesis on the development of frameworks to inform the efficient
placement of detection stations so as to improve monitoring programs for AIS.

If forecasts can be made about the likely location of an invader then monitoring
effort can be optimized to preferentially look where target species are likely to
occur. A classic concept from early ecological theory is that species occur in areas where the environmental conditions are suitable, given their intrinsic biological tolerances. Grinell considered that species would fill all of their suitable habitats (the “fundamental niche”). In addition to abiotic factors like temperature, biotic interactions such as predation and competition can shape species distributions; Hutchinson felt species would be excluded from part of their fundamental niche by biotic interaction and defined the realized niche (Silvertown 2004). Indeed, models of species distribution (SDMs) that rely on niche concepts are used extensively – and successfully (reviewed in Guisan and Thuiller 2005; Richards et al. 2007) – in ecology and conservation biology (Guisan and Thuiller 2005). These models tend to assume that observed species distributions represent the realized niche and correlate observed environmental variable with occurrence.

SDMs do not incorporate information on points of introduction and subsequent dispersal processes into their predictions (Araújo and Guisan 2006). Logically, a species must be transported to an area of suitable conditions before it can occur there and there is no assurance that all suitable habitats will experience dispersal, and thus may not be occupied (Shurin 2000). At the extreme end of opposition to niche models are neutral models in which species simply disperse,
and where individuals show no preference for environment. These models are the anti-thesis of niche models and are not readily falsifiable (McGill et al. 2006). The mechanism structuring species distributions is likely some combination of dispersal and environment and statistical techniques are available to examine the relative importance environmental heterogeneity and dispersal limitation (Borcard et al. 1992). Applications of these types of tools tend to show importance of both environment and dispersal (e.g., Gilbert and Lechowicz 2004).

Chapter 1 extends traditional species distribution models by combining two sub-models: the first, a traditional SDM that models realized niche by correlating environmental variables with species abundance and the second that accounts for the dispersal limitation that further constrains the distribution of species by making use of larval distances from adult sources. I show in Chapter 1 how such a joint model can be constructed and fit. The model I build has clear biological meaning and can capture the fecundity, dispersal, environmental preference, and conspecific aggregation of a target species, while retaining a strong resemblance to traditional SDMs. Therefore, this extended SDM can be built using common statistical packages that users of traditional SDMs are already familiar with. I show how the parameters it captures can be used to forecast larval locations and generate monitoring programs.
I apply the model to distribution data of *Ciona intestinalis* (henceforth *Ciona*) an invasive tunicate species that is threatening bivalve aquaculture in eastern Canada, causing increased costs to farmers there via loss of crop, and increased processing costs (Paetzold et al. 2012). *Ciona* is an invertebrate urochordata, or sea squirt that is found around the world. *Ciona* has a sessile adult stage and disperses via a lecithotrophic (non-feeding), planktonic larval stage, resulting in a relatively short planktonic duration (less than a week [Dybern 1965; Svane & Havenhand 1993]) and, therefore, an inability to naturally disperse long distances. The short dispersal range of *Ciona*, and its high-fecundity (approx. 12,000 eggs/adult; Carver 2003) and rapid maturation (approximately 1-2 months [Yamaguchi 1975]) has contributed to its success as a problematic invader. *Ciona* occurs in Boughton Bay, PEI whence Collin et al. (in press) collected distributional data and where I apply advanced correlo-mechanistic SDM model to show how the model captures biological attributes of *Ciona* and how the model can be used to design monitoring programs for other bays.

Chapter 2 develops a framework to compare models of larval dispersal. Given the importance of dispersal in monitoring demonstrated in Chapter 1, this framework can therefore be used to compare the utility of various models to inform monitoring programs. The motivation in comparing these models is to
examine the value of statistical versus mechanistic models of larval dispersal. The relative importance of these two types of model is a broad question in ecology in marine and terrestrial systems. Early, simple models of seed dispersal were adapted to include more features of physical dynamics like resistance and turbulence in terrestrial systems (Nathan et al. 2011). Empirical studies examined the distribution of seeds away from parent trees and fit these patterns to statistical kernel functions (Nathan and Muller-Landau 2000). Studies of larval dispersal in marine systems have lagged somewhat behind, but face the same duality of statistical versus mechanistic models of dispersal, and the two are not often compared (Cowen and Sponaugle 2009).

In marine systems, statistical kernel-based models are popular and mechanistic models are often hydrodynamic model of water currents which presumably steer the transport of larvae. Hydrodynamic models estimate the entire path of a larva and the processes which drive that motion, whereas statistical dispersal models estimate the net outcome of that movement. There is reason to suspect the ability of hydrodynamic models to capture the detailed movement involved in biological processes. This is due to the simple fact that many biological processes governing larval transport like pelagic duration, vertical migration, or environmental cues are poorly understood (Delaney et al. 2012) and are
therefore either not included or coarsely approximated in these hydrodynamic models – often leading to poor performance (Roughan et al. 2011).

Due to possible shortcomings of these hydrodynamic models, validation of their results should be demanded, however many biological studies implement expensive, complex hydrodynamic models with insufficient validation (Arhonditsis et al. 2006) and there are numerous calls in the literature to validate these methods (Haase et al. 2012), but validation of hydrodynamic models is challenging due to the incompatibility of field data and model data. Empirical data rarely captures the path that larvae travel and more often capture the outcome of this movement in the final resting points of larvae. These resting points reflect the dual constraints of the realized niche and dispersal – the environmental conditions into which the larvae are transported affect their probability of recruiting. Because hydrodynamic models do not typically model the probability, recruitment data (larvae that are transported, settle and develop) typically collected in biological studies and the paths of larval transport generated by hydrodynamic models are of a fundamentally different form and are not always comparable (Metaxas and Saunders 2009).
Drawing from SDM experience in Chapter 1 I demonstrate a technique to scale this larval transport data generated by a hydrodynamic model to be comparable to recruitment data, collected in a biological survey and demonstrate how this could be used to validate hydrodynamic models. This technique allows comparison of hydrodynamic or other models of dispersal with differing types of output data and allows me to demonstrate a comparison between the results of a hydrodynamic model to a statistical one derived from results in Chapter 1 and demonstrate how these statistical models can be used as alternative models against which the performance of a hydrodynamic model can be compared.

The chapter compares three models: i) a statistical SDM of just environmental data; ii) the joint statistical model like that in Chapter 1; and iii) a mechanistic model implementing a sophisticated hydrodynamic particle tracking program. Because of the robust level of recruitment data available of *Ciona* in PEI and the ability to scale model transport data I am able to perform extensive comparisons. The many metrics all suggest the same conclusion: correlo-mechanistic statistical models drawn from recent advances in SDM may perform as well as hydrodynamic models and, at least, should be considered as alternative models to complex, expensive hydrodynamic dispersal models. This chapter introduces a
framework for comparison among statistical and hydrodynamic models and encourages more such comparisons in the future.

Advances presented in the first section of my thesis optimize the detection of AIS. The second section of my thesis is concerned with what an appropriate management response is following detection. Predictably, the complete removal of an invader (i.e., eradication) is the response that can best limit damage. Eradication is an eminent idea in invasion biology and is often an explicit goal of government (Genovese and Shine 2004). However, there are few examples of success (see Mack et al. 2000 for a review), especially in marine systems (but see Culver and Kuris 2000, Bax et al. 2002, Miller et al. 2004, Wotton et al. 2004, Anderson 2005). The few marine successes have typically occurred in the early stages of invasions; after establishment and initial spread, eradication is typically no longer considered.

I argue that eradication has been prematurely dismissed in practice due to the lack of practical, quantitative steps for management. The few papers that have examined this important issue have provided general heuristics regarding eradication success [e.g., it is early in an invasion (Simberloff 2003); the species has biological characteristics susceptible to control (Myers et al. 2000); rates of
removal are greater than rates of reproduction (Bomford and O'Brien 1995); see Appendix B for more]. While these heuristics are useful, they provide little instruction on the practical elements of eradication, that are of more interest to managers such as cost, scope, and time and research required. Explicit frameworks need to be developed to fully evaluate the potential for eradication and to provide managers these useful parameters.

Chapters 3 and 4 develop such a framework. Chapter 3 introduces the first quantitative framework for eradication of invasive species. It exploits the life cycle of the species and variation in vulnerability with age (Buhle et al. 2005) in order to disrupt reproduction and eradicate, even if all individuals are not directly vulnerable to treatment. It uses basic ecological principles like those present in population viability analysis but designed to guide managers in an eradication campaign. It demonstrates how with basic biological data on maturation rates a manager can calculate the number and frequency of repeated treatments passes required to eradicate a species. When there are multiple populations the framework demonstrates how to schedule treatments spatially. It defines specific limits for eradication: the treatment must be effective on (at least) pre-reproductive individuals and treatments must be completed on all populations before any missed pre-reproductive individuals in the first population mature.
Thus, for the first time, it allows managers to test the feasibility of eradication empirically with a minimum of data. I applied the framework to a high-profile invader and showed how eradication of *Ciona* is feasible and I generated an actionable eradication plan. I also showed how from a bio-economic perspective, due to the high value of *Ciona* aquaculture compared to the cost of eradication, eradication of *Ciona* is optimal and only requires a 16% chance of success.

Chapter 3 was an exciting contribution to invasive species management, but it was not without limitations. It only implicitly recognized the importance of delimitation; it was designed only for sessile species, and did not consider spatio-temporal variation in treatment efficacy or vulnerability. Also it did not integrate itself with other available eradication frameworks. Chapter 4 aims to fill these gaps and create a more complete eradication framework. The chapter gathers 43 eradication guidelines from dozens of published eradication frameworks (including Chapter 3) and applies them all to an ongoing invasion in California. I find that even in combination existing frameworks are unable to provide complete guidance to manage the invasion. I then distill the key elements from all the frameworks and extend them so as to create a meta-framework that can address the invasion and possible help eradicate other species elsewhere.
In addition to being a review of eradication frameworks, Chapter 4 addresses all the limitations of Chapter 3, and includes guidance from other frameworks as well. It identifies areas where the existing frameworks disagree, as well as discarding suggestions from them that are not required, thus accelerating analysis of eradication. It identifies gaps in their recommendations and patches them and includes useful legal, administrative, and post-planning suggestions not included in Chapter 3. The entire framework is generalizable and is presented concisely and accessibly in an adaptive decision tree (Figure 1 in Chapter 4). Thus rather than a collection of competing, occasionally contradictory frameworks I offer a single framework that consolidates all of the available guidance.
References


**Linking statement 1**

The goal of the first section of my thesis is to improve detection programs for aquatic invasive species. The first chapter investigates the benefits of creating a joint model that combines dispersal potential and environmental tolerances to predict the locations of, and thus inform detection of, invasive species. This model takes a statistical approach, incorporating a dispersal kernel to estimate the movement of larvae in a marine system. I show how this combined model of dispersal and environmental preference captures recruitment patterns, and uses it to design a monitoring strategy for invasive tunicates. This is a substantial advancement in the field of species distribution modeling and invasive species monitoring.
Chapter 1
Capturing dispersal patterns and tolerance of early invaders with enhanced species distribution models: applications for design of detection programs.

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Abstract

I aim to improve detection programs for aquatic invasive species at small scales. I investigate the benefits of creating a model that combines of dispersal potential and environmental tolerances of invasive species. I show how this joint model captures recruitment patterns, and use it to design a monitoring strategy for a nearby, at-risk bay. Spatial patterns of recruitment and temperature was collected in Boughton River and temperature patterns were collected in St. Peters Bay; both in Prince Edward Island, Canada in 2008 and 2012.

This model approach is based around a simple framework that can be easily adapted to different species characteristics (e.g., dispersal patterns, larval behaviour) and different environments. I built joint correlative-mechanistic models and fit them to adult location and recruitment data from an early invasion of the vase tunicate, *Ciona intestinalis*, in Boughton River. These models allow construction of a probability of detection model to compare different monitoring scenarios. My joint model was better able to capture patterns of recruitment than an environmental model and was equally powerful as a GLM. Larval recruitment showed a clear hump-shaped dispersal kernel. Application of the probability of detection model to St. Peters Bay identified areas where monitoring could be most effective. Probability of detection maps indicate that monitoring programs
informed by my correlo-mechanistic model could improve the probability of detection.

1.1 Introduction

Aquatic Invasive Species (AIS) threaten coastal diversity and commerce worldwide (Carlton 1993; Mack et al. 2000; Ruiz et al. 2000b; Occhipinti-Ambrogi and Savini 2003). AIS can affect the recipient community in many ways: they can out-compete local species for resources (e.g., food, space), alter local environments (Cuddington & Hastings 2004), and carry harmful pathogens (Ruiz et al. 2000a; Minchin 2007). Additionally, AIS can affect commercially valuable species, where economic costs can reach billions of dollars (Aukema et al. 2011). The increasing rate of global introductions (Ruiz et al. 2000b) compels us to devise management action that can reduce, if not prevent, the impact of AIS on local communities and human activities.

To control AIS I must be able to monitor effectively (Vander Zanden et al. 2010) and detect invasions as early as possible, prior to widespread impacts. The invasion process can be divided into the following stages: (1) transport and introduction, (2) local establishment, (3) regional spread and (4) population growth to nuisance levels (MacIsaac et al. 2002; Blackburn et al. 2011), so we
can identify the most appropriate stage for action. Intervening during the transportation phase is the most effective approach for managing AIS (i.e., prevention is better than cure; Leung et al. 2002), but despite current efforts, invasions still occur (Lodge et al. 2006). Therefore, early detection at the point of introduction, prior to widespread establishment, is the next best option. Early detection, coupled with effective control, can slow the spread (Sharov and Liebhold 1998) and reduce, if not entirely prevent the impacts of even the most problematic AIS (Naylor 2000; Brooks et al. 2004). Thus, research that can optimize monitoring effort and which increases the probability of detecting small populations will be highly beneficial to managers tasked with designing monitoring strategies.

A key attribute of an effective monitoring strategy is optimal allocation of limited resources (Delaney and Leung 2010). Frameworks that can guide and optimize effort allocation will lead to a higher probability of detection at a lower cost (Leung et al. 2004). At present, monitoring effort is justifiably focused on areas of high introduction risk or high value (Ricciardi and Rasmussen 1998; Hauser and McCarthy 2009). Monitoring programs are often designed for large-scale regions – typically at the scale of a regional authority, but invasions begin on small scales, often confined to a single point of introduction (e.g., harbour or a bay) –
the same scale at which treatment is most likely to succeed. Early detection and subsequent treatment are possible only if small-scale monitoring techniques are effective. However, since there are few studies that provide small-scale guidance for environmental managers, monitoring efforts tend to be rather haphazardly assigned (Fox et al. 2009).

Species distribution models (SDMs) are commonly used to identify areas at risk of invasion. Though sometimes criticised as ecologically naïve (Davis et al. 1998; Pearson and Dawson 2003; Franklin 2010), SDMs have repeatedly proven their value (e.g., Herborg et al. 2009; reviewed in Guisan and Thuiller 2005; Richards et al. 2007) and remain an important tool for allocating monitoring effort. With respect to their application to early detection and their utility in allocating search effort, I feel the SDM literature has four critical limitations: (1) SDMs have been criticized for their inability to extrapolate to new environments, taking a correlative approach (Pearson et al. 2006; Franklin 2010); (2) the regional extent of most SDM studies exceeds the small-scale of AIS spread during the early stages of invasion (Seo et al. 2009). The scale at which a SDM is constructed can affect its results (Zimmerman et al. 2010), but their efficacy is largely untested at small scales, the very level at which much management is undertaken; (3) SDMs do not adequately incorporate information on points of introduction and subsequent
dispersal processes into their predictions (Araújo and Guisan 2006); and (4) SDMs are rarely explicitly designed to model the environmental tolerances of the larval stage of a focal species. Larvae – usually numbering several orders of magnitude more than adults – will disperse farther and wider than their source adult distribution and may thus be an easier target for detection. I feel early detection will be aided by incorporating dispersal and examining the detection of early larval stages of invaders. These last two limitations highlight the importance of dispersal in the invasion process. Dispersal is of general ecological importance (Kinlan and Gaines 2003; Palumbi 2003) but its role in early range expansion is of particular importance to AIS. Range expansion (and the dispersal processes underlying it) is ignored by simple SDMs, thereby losing the opportunity to target where within its potential range an AIS is most likely to be found at the start of the invasion.

SDMs model only the realized niche and assume species occupy all suitable habitats at equilibrium (Guisan and Thuiller 2005). Early stages (i.e., early establishment and local spread) of invasion are small and localized and can be dispersal limited, and species occur only where suitable habitats fall within the species dispersal range (Cain et al. 1998; Moore and Elmendorf 2006; Münzbergová and Herben 2005), thus invasion patterns may not be captured
well by traditional SDMs, leading to false-positives (i.e., suitable habitats that are not inhabited). SDMs that include dispersal or other ecological factors may aid the detection of early invaders. At present there are few studies that model patterns of AIS using dispersal and quantitative environmental preferences outside of the terrestrial realm (Robinson et al. 2011) (but see Leung and Mandrak 2007) and none have considered ontogenetic shifts (shifting tolerances at various life stages; Robinson et al. 2011). For example, Inglis and colleagues (2006) compared the efficacy of a qualitative habitat suitability index (HSI) and quantitative tolerance models within a bay. They combined these with an oceanographic dispersal model and were able to make reasonable predictions of adult locations of two invaders, albeit with low sensitivity. Trebitz and colleagues (2009) investigated the ability of various habitat attributes to predict species richness within a small watershed. None of the tested variables showed strong correlation with benthic AIS richness. These studies provided valuable guidance for AIS detection, but leave room for more research. Each study struggled to find strong relationships, only one accounted for dispersal limitation, and neither adapted their results to the design of future monitoring plans. The paucity of studies and their limited success has prompted a recent call in the literature for more such studies (Robinson et al. 2011) and integration into early detection strategies.
Dispersal will affect monitoring strategies in two ways: first, it will define the optimal distance for sampling near likely points of introduction, and second, knowing the expected larval dispersal distance allows sampling techniques to target both adult and larval stages. There are many ways to detect dispersing AIS source populations: propagules can be detected by filtering water samples (e.g., Kraft and Johnson 2000) or DNA sampled in the environment (so called eDNA); e.g., Lodge et al. 2012), recruits can be detected on dedicated collectors (e.g., Delaney et al. 2012), and adults can be found in habitat surveys (e.g., Simkanin et al. 2012). While surveying for adults is possibly simpler, sampling for propagules and recruits (or possible eDNA) increases the area that can be gainfully sampled as the distribution of propagules normally far exceeds the distribution of adults (Kraft and Johnson 2000). Regardless, all targeted life stages have the same limitation: where is sampling effort most effectively allocated? If patterns of dispersal could be predicted, they could then be used to refine a general SDM and identify optimal locations for monitoring efforts. By creating a flexible framework that can be easily adapted to match the dispersal characteristics of a target species, I could provide monitoring guidance for numerous species in many different environments.
I constructed a model that tests the applicability of SDMs at small scales, which includes both dispersal and environmental tolerances and is capable of forecasting optimal locations for sampling. It is not clear from the literature how dispersal should be included – whether as a component of a traditional SDM or as a sub-model (Leung et al. 2012), so I explore both possibilities. My model is an application of well-established generalized linear models (GLMs) (see Guisan and Hastie 2002), but specifically re-cast for application to monitoring strategies and to maximize biological interpretability of the model equations. To demonstrate its utility in real-world applications, I fit my model to field data of a recently introduced high-impact AIS and show how the results can be extrapolated and applied to generate monitoring programs in other at-risk areas.

1.2 Methods

First I will introduce my study system and species and then my modified SDM that will estimate the recruitment of a target species at a site with a detection station (and a given set of environmental conditions there). I will then show how this modified SDM can be fit with standard maximum likelihood techniques and how the fitted model can be used to estimate the probability of detection for a candidate monitoring program.
1.2.1 Study species and system

I parameterized my model with distributional data of the highly invasive tunicate, *Ciona*, previously collected by Collin et al. (in press) in Boughton River, Prince Edward Island (PEI), Canada. *Ciona* is a particularly problematic AIS in eastern Canada (Howes et al., 2007) and was first detected in PEI in 2004 (Locke et al. 2007). Since its introduction, *Ciona* has successfully established populations in seven inlets in PEI and threatens further spread. It has created serious economic problems for the blue mussel (*Mytilus edulis*) aquaculture industry by fouling the crop and equipment (Ramsay et al. 2008), causing production loss and additional maintenance costs.

*Ciona* has a sessile adult stage and disperses via a lecithotrophic (non-feeding), planktonic larval stage, resulting in a relatively short planktonic duration (less than a week [Dybern 1965; Svane & Havenhand 1993]) and, therefore, an inability to naturally disperse long distances. Collin et al. (in press) previously fit a dispersal kernel for this system and found a dispersal range of < 5 km. The short dispersal range of *Ciona*, and its high-fecundity (approx. 12,000 eggs/adult; Carver 2003) and rapid maturation (approximately 1-2 months [Yamaguchi 1975]) has contributed to its success as a problematic invader.
Fieldwork was conducted in Boughton River, a small, 6 km-long, semi-enclosed estuary on the eastern coast of PEI (Figure 1.1). Boughton River has generally modest currents driven by tidal changes rather than a strong unidirectional flow like many other rivers. *Ciona* was first detected there in the fall of 2007 (two recruits, G. Arsenault, pers. comm.), and data on the adult distribution and subsequent larval recruitment were collected in summer 2008 (Collin et al. in press). Each of 33 surveys conducted in June prior to recruitment (Ramsay et al. 2009) consisted of a 50-m transect, which ran horizontally through a mussel lease, starting from a haphazardly-chosen location. The total number of adult *Ciona* present on the equipment, mussels and substrate directly below was recorded. In August of 2008, soon after *Ciona* became reproductively active, a large ‘grid’ of sampling stations (88; Figure. 1.1a), each containing a 20x20 cm PVC plate at 2-m depth, was deployed for two weeks. Upon collection, the total number of *Ciona* recruits on each plate was counted using a stereomicroscope.

PVC settlement plates provide a suitable substratum for larval settlement and are commonly used for larval monitoring (e.g., Clark and Johnson 2011; Crooks et al. 2011; Lacoursière-Roussel et al. 2012). However, the surrounding environmental conditions also play an important role in settlement (Pawlik 1992) and, therefore, temperature and salinity data were also collected in Boughton River using a SeaCAT CTD in 2008 during collection of the sampling collector grid. These two
variables are the most important influences on marine life (Tyberghein et al. 2012) Values were average from three depths: 2 m and 2 m +/- 0.25 m.

1.2.2 Joint dispersal-tolerance model: theoretical development and testing

A single adult within a bay would release some number of propagules that are later detectable (i.e., survive the dispersal process and recruit so they can be collected by the relevant sampling technique), I define this as the effective per-adult fecundity.

The expected value of recruitment on the \( i \)-th detection station, \( S_i \), is

\[
E(S_i) = AJ\text{Wei}(\bar{D}_i; k, \lambda)f(\bar{E}_i)
\]

1.1

This equation assumes that each of the \( J \) adults sources are of equal population size (number of adults), \( A \), and have a per-adult fecundity of \( n \). The first term of the model, \( AJn \), estimates the total number of larvae prior to dispersal. Without this simplifying assumption, the equation is difficult to fit with standard tools since it has many non-standard variables. Without this assumption coefficients for the size of each adult population, \( A_j \) would have to be fit. This equation also expresses the distance of the \( i \)-th station from each adult source as the mean of all \( J \) adult-station distances, (the mean distance the \( i \)-th station lies from adult sources). This avoids further having to fit adult-station distance coefficients.
\( \text{Weibull} \) denotes the Weibull function, a distribution that is able to capture diverse forms of dispersal (Morales and Carlos 2006). The Weibull function takes parameters \( k \) and \( \lambda \) which control the shape of the distribution – allowing it to assume a decay-curve shape or a hump-shape with distance. This number is scaled twice by multiplying it first by \( \text{Weibull}(D_i;k, \lambda) \), which scales the dispersal according the mean distance the station is from the source, then again by \( f(E_i) \). This final term scales the arriving larvae by their probability of recruitment as a function of the environmental conditions at station \( i \), \( E_i \).

In order to estimate the recruitment on a station, \( S_i \) in equation 1.1 I must define the probability of recruitment function, \( f(E_i) \), from that equation. This term must be strictly bounded \([0,1]\). I model this as,

\[
f(E_i; \beta_1, \beta_2) = \frac{e^{\beta_1 E_i + \beta_2 E_i^2}}{\sum_i e^{\beta_1 E_i + \beta_2 E_i^2}}
\]

with fit parameters \( \beta_1 \) and \( \beta_2 \) indicating the overall shape (mean and variance) of the species environmental response. This exponential linear equation was chosen to accommodate a potential mid-level response to temperature and to correspond with the form of a standard GLM with log-link so they may be compared. The denominator scales the whole term so it is bounded at \([0,1]\). If I replace the constant \( AJn \) with the propagule pressure constant, \( \phi_0 \), then the expected value of recruitment becomes,
Equation 1.3 is the final form of my modified SDM made by making two substitutions in equation 1.1 for the propagule pressure constant, $e^{\beta_0}$, and for the probability of recruitment function (equation 1.2). The equation includes a function of the local environment (the third term with $E_i$) that scales the probability of recruitment according to the environmental conditions at the station. Equation 1.3 is the product of three exponential terms (the Weibull distribution is among the exponential family of distributions) and is similar to a standard form of generalized linear model (GLM), with an expected value of,

$$E(S_i) = e^{\beta_0} e^{\beta_i D_i + \beta_i E_i} e^{\beta_i D_i + \beta_i E_i}$$

1.4

In both equations 3 and 4 the second and third terms are curvilinear exponential functions of distance and environment respectively, with the first term as a propagule pressure constant. With assumptions about adult population size and average distance this modified equation 1.3 can be fit by common statistical packages, just like a GLM (equation 1.4). Further, in my formulation each exponential term has a clear biological meaning and sensible bounds.
I use a negative binomial error structure since it is recommended for analysis of count data (Zuur 2009) and it allows an additional over-dispersion parameter $\theta$ which can fit higher variance than supported by the binomial – biologically, this relaxation of binominal assumptions can be interpreted as aggregation (conspecific repulsion or attraction of subsequent recruitment after initial recruitment).

I fit four different models. The simplest was a GLM using just temperature and salinity – the two of the most important influences on marine life (Tyberghein et al. 2012). I also fit the GLM shown in equation 1.4. I fit my modified model in equation 1.3 with maximum likelihood using the likelihood function,

$$
\log(L) = \sum_i \log\left(\text{NegBin}\left[S_i; \mu, \theta\right]\right)
$$

$$
\mu = e^{\beta_0} \frac{e^{\beta_1 T_i + \beta_2 S_i}}{\sum_j e^{\beta_1 T_j + \beta_2 S_j}} \text{Wei}\left[\bar{D}_i; k, \lambda\right]
$$

with both binomial and negative binomial error structure to examine the effect of over-dispersion. When using binomial error structure I rounded down non-integer values of expected recruitment. All GLMs were built using the R program (R Core Team 2012) following Zuur et al. (2009). I also examined the spatial auto-correlation of the residuals for each model using Moran’s $I$ to identify any remaining, un-modeled spatial auto-correlation in the models.
My modified SDM model (equation 1.3) extends naturally to the generation of
detection strategies. It estimates the number of recruits at the $i$-th detection
station. I can thus estimate the probability of a station having zero recruits. The
complement of this probability is the probability of detecting one or more recruits
at that station. I can estimate the total probability of detection, $P_d$, for a set of $Q$
detection stations by estimating the probability of any of the $Q$ stations having
one or more recruits,

$$P_d = 1 - \prod_{i=0}^{Q} \text{NegBin}(0; \mu_i, \theta)$$  

1.6

The environment at each detection station and the dispersal there will control the
detection probability. The total probability of detection is the probability of
observing one or more recruits on any of the $Q$ stations. Thus by estimating the
dispersal and environmental tolerance of a species, one can make a priori
predictions about the relative efficacy of a given detection program.

1.2.3 Extrapolation of model to design monitoring strategy

Using the fit parameter values from the best fitting model of Boughton River data,
I estimated the spatial distribution of detection probability in St. Peter’s Bay, PEI,
another bay at risk of Ciona invasion. St. Peter’s Bay is $< 30$ km from Boughton
River, comparable in size, and also used for aquaculture. A caveat of the
extrapolation is that the fitted propagule pressure value ($e^{\theta_0} = AJn$) is assumed
constant between the two bays – if this is not true, as is generally likely, then probability of detection values are valid only in a relative sense. Environmental data (temperature and salinity) from 2-m depth were collected at 22 locations in St. Peter’s Bay on August 23rd, 2012. These data were interpolated by kriging to create a 25m grid over the entire bay. Past monitoring programs have targeted areas of high human activity as likely introduction sites (e.g., docks and wharves for *Ciona*; Lambert et al. 2005), so I used all eight boat launches in St. Peter’s Bay as potential adult sources and estimated relative probability of detection throughout the bay based on each dock as an initial introduction site. The launches are not suitable substrate, but I presume adults can occur on suitable substrate near each launch (i.e., moored boats, loading docks).

1.3 Results

1.3.1 *Ciona* survey results

1.3.1.1 Adult distribution

*Ciona* was found in 10 of the survey transects and their locations were mapped. The population sizes were small, with a mean number of 2.5 and a maximum of 40. The adult locations were predominantly in the north-west of the bay with some populations near the center.
1.3.1.2 Patterns of larval recruitment

Of the 88 settlement plates deployed, a total of 82 were recovered, and *Ciona* recruitment occurred on 66. The average number of recruits was 9.1, with a maximum count of 49. Recruitment was generally concentrated towards the western end of the bay.

1.3.2 Model results

1.3.2.1 Environmental models

All four environmental models of recruitment were quite predictive, with the worst model explaining 55% of variation in recruitment (Figure 1.2). The GLM with just temperature and salinity was the worst model (the highest AIC: 450, and lowest R²: 0.55; Figure 1.2a, “GLM-TS”, Table 1.1). It was also the only model with significant auto-correlation in its residuals, and had the lowest R². The GLM model with environment and mean distance and the modified model with probability of settlement and Weibull dispersal were very similar: their AIC values differed by 0.1, they had nearly identical R² values (0.61), and neither had significant spatial auto-correlation in their residuals (Figure 1.2b,c; “GLM-TS+D” and “ProbWeibTSD”, Table 1.1). With distance included, salinity was removed from the model as it offered no additional power. When the binomial distribution replaced the negative binomial as a model for error, the model was able to make
good predictions of recruitment (R²=0.62; Figure 1.2d, “BinomPWTSD”, Table 1.1) with no spatial auto-correlation in its residuals. Auto-correlation present in the data, but not present in the model residuals would indicate the model had properly accommodated the spatial structure of the data (Wagner and Fortin 2005). Furthermore, the predicted values made by the model with binomial error were almost identical to the predicted values of the negative binomial model (r=0.99; p<1E-10). The residual variance around those means values was, however, greater than expected by the binomial model. Due to this, the AIC of the negative binomial model was much lower than the binomial model (402 vs. 446) though their predictions are almost identical.

I summarize the best fitting parameters from the model “ProbWeibTSD” below and in Table 1.2.

1.3.2.2 Environmental tolerance

The fit parameters indicated a peak recruitment probability of 0.025 at 23.5 °C (Figure 1.3). The distribution is hump-shaped falling to low probability of recruitment near 20 °C. This relationship is given by the fit parameters β₁ and β₂ in equation 1.3.
1.3.2.3 Dispersal kernel

The Weibull function describes the proportion of larvae that travel a given distance (the dispersal kernel). The shape of this curve is defined by the two Weibull parameters, shape ($k$) and scale ($\lambda$) shown in equation 1.3. The fit kernel parameters indicate a spatial lag, peaking at a mean distance of about 1.6 km from the adult source (Figure 1.4).

1.3.2.4 Life history

The over-dispersion parameter ($\theta$, equation 1.3) fitted was 5.98 indicating slight aggregation in the recruitment data (Lloyd-Smith 2007). *Ciona* may release larvae in cohesive packets held by mucus, which could help to explain this apparent aggregation. The propagule pressure scalar, $e^{\beta_0}$, yielded a reasonable fit value of 1873 – this is the total number of propagules available to all plates after larval mortality and before being scaled by distance and probability of recruitment.

The dispersal modeled in equation 1.3 is the result of a time-integrated dispersion over the two weeks that the plates were deployed in Boughton River, a limitation of the data itself. Therefore, the dispersal parameters should be interpreted as the outcome of two weeks of recruitment (i.e., cumulative recruitment of competent larvae produced in this period). This is longer than the
dispersal period of individual larvae, but is shorter than the generation time, so patterns of recruitment will not be confounded by new adults. My estimate of fecundity is, however, based on the number of larvae that reach a plate over two weeks (i.e., “functional fecundity”), rather than the true fecundity of which I have no direct measure.

1.3.3 Application to St Peter’s Bay

Based on temperature and the distance from presumed adult sources in St. Peter’s Bay, and using fitted values from equation 1.3 for Boughton River, I calculated the probability of a given location in St. Peter’s Bay having one or more recruits detected (i.e., a detection) by inputting the temperature and distance to adult source of each site into equation 1.6. The resulting probabilities of detection in St. Peter’s Bay are based on an invasion of the exact same size as in Boughton River. Since this is an unlikely assumption I treat the predicted probabilities of detection only as relative strengths of detection. I performed this calculation for every grid location in St. Peter’s Bay and from these probabilities I built a map of probability of detection. I varied the presumed adult source site for each likely introduction site in St. Peter’s Bay and re-calculated the probability map, yielding maps of relative detection probability based on many possible introduction sites (Figure 1.5). The maps show complex patterns of detection
where monitoring effort should be concentrated. For some introduction sites (e.g., Figure 1.5f) in areas of homogenous temperature, detection probability was guided only by dispersal, leading to ring-shapes of fixed radius. Other areas where temperature was more suitable near the introduction site (Figure 1.5a,e), led to irregular shapes where competing influence of dispersal and temperature tolerance interplayed. The net strategy (Figure 1.5i), calculated by presuming all possible adult sources became infested, suggested one specific area for monitoring.

1.4 Discussion

The main aim of this study was to compare the efficacy of different SDMs at small scales and to provide a better conceptual framework to managers for optimizing early detection programs for invasive species. Typical SDMs are used to model the probability of occurrence of a species in a given location. The simplest SDM that used only temperature and salinity was promising, but it was unable to capture the spatial structure of the data (as indicated by the spatial auto-correlation present in its residuals). By further adding a kernel function to model dispersal from introduction sites at local scales, I improve my ability to model recruitment patterns and hence detect invasive species, without concerns of spatial auto-correlation. The improvement of SDMs by addition of distance has
been observed in other systems (e.g., Allouche et al. 2008) but has not been
demonstrated at the small scales over which invasions occur. Traditional SDMs
aim to predict the probability of occurrence at a given site, but ours aims to
predict abundance, use dispersal to improve its forecasts and includes an explicit
probability of detection model to evaluate monitoring (equation 1.6). I suggest
that for newly established populations of AIS, environmental parameters are
important for guiding effort to detect recruits, but their influence can be
superseded by spatial influence of dispersal.

My approach is sufficiently general to incorporate the dispersal and tolerance of a
wide range of species that have a sessile or sedentary adult phase and disperse
via a planktonic stage (e.g., many benthic invertebrates, macroalgae, and some
fish). My framework could be used to design monitoring programs for other
harmful invaders and the systems they place at risk. My recasting of GLM SDMs
allows for easier biological interpretation with no loss in power. I was able to
estimate a probability of settlement based on temperature, the functional
fecundity of the target species, and its average dispersal kernel. The result of
these fitted equations was a correlo-mechanistic model of species dispersal and
recruitment. While still ultimately a correlation model, it can approximate the
features of a true mechanistic model (e.g., a hydro-dynamic, individual-based
model; see Chapter 2), but which is simpler to fit. It captures the mechanism of recruitment: dispersal from sources, proportional to distance followed by temperature-specific recruitment. Thus it approximates the potential process of a mechanistic model, but is still fundamentally correlative. These equations allow maximum likelihood fitting and the generation of probability of detection maps for at-risk sites. The classical GLM only needs a few simple algebraic changes to be used to fit a correlo-mechanistic model of recruitment and dispersal. The resulting model is built from biological fundamentals: i) that larvae from an adult source will disperse proportional to distance, according to the life history of the species; and ii) larval recruitment on a plate is influenced by the surrounding environmental conditions. Mechanistic models have received increasing attention in the literature (Leung and Mandrak 2007; Kearney and Porter 2009; Leung et al. 2012). There is much debate in the literature about when correlative models should be dismissed in favour of mechanistic ones (Franklin 2010), but in some instances they are essentially one in the same.

Beyond the structural improvements to the SDM, another improvement to my approach was the focus on monitoring for propagules rather than adults. Although adults will precede larvae in many invasions, searching for propagules (e.g., larvae) is likely to be more efficient early in an invasion (Kraft & Johnson
2000), due to the high number of propagules compared to adults. In aquatic systems, detection of adults often involves SCUBA teams searching limited areas for small numbers of adults. This approach allows earlier searches, prior to the reproductive season, but can be costly and challenging. For my case study, *Ciona* is reproductive from July through to October (Ramsay *et al.* 2009) so a monitoring program targeting *Ciona* larvae (e.g., plankton sampling, recruitment plates) would be fruitless before July. However, after July such detection would be more probable due to the large number of larvae (especially if guided by my framework) and would be inexpensive compared to SCUBA teams. Thus, there may be a trade-off between costly, early SCUBA surveys for adults, with a lower chance of detection, or later, less expensive larval surveys, which can yield a higher probability of detection. Post-detection management would be cheaper if the adults are detected and removed before they reproduce (Edwards and Leung 2009; Chapter 3), but ensuring all adults have been removed prior to reproduction is difficult and the number of times this is achieved in practice is vanishingly small. Early detection of adults is rare in general, including with the popular “bio-blitzes” approach where groups of divers, taxonomists, and volunteers search for adult invaders (Cohen *et al.* 2011). Currently only 18% of AIS monitoring efforts rely on recruitment plates (Campbell *et al.* 2007), and
research aimed at improving the efficacy of plate techniques could widen their usage and lead to earlier, less costly detections of AIS.

Previous attempts to model dispersal at a small scale or for management application have taken different approaches. Kanary et al. (2011) built a fully mechanistic model by combining a matrix model with a hydrodynamic model. They showed how dispersal of *Ciona* in another PEI bay was limited and likely needed intermediary substrate to disperse out of the bay. Other authors who have taken statistical approaches have found spatial auto-correlation to be a serious problem in GLM SDMs (reviewed in Dormann et al. 2007). They review several common techniques to remove this influence, but note that these tools do not directly capture dispersal, which can be a cause of the spatial auto-correlation. Diebel et al. (2009) found that the inclusion of spatial auto-correlation into an environmental model greatly improved their predictive ability, consistent with my finding that inclusion of dispersal distance removed spatial auto-correlation from the residuals of my SDM. My model addresses historic absence of dispersal limitation in SDMs (Guisan and Thuiller 2005) and builds upon work by Leung and Mandrak (2007) to answer a call for monitoring advice in the literature (Fox et al. 2009).
The system from which I parameterized my model had only a narrow range of observed temperatures which may limit my ability to extrapolate beyond this range. Boughton and St. Peter’s had comparable temperature ranges (20.5-24.4 °C and 21.2-24.8 °C, respectively). Indeed, the modeled response of larvae to temperature has a narrower range than the published limits of adult tolerance (Vercaemer et al. 2011). In particular, my model predicts very low recruitment at temperatures below 20ºC (Figure 1.3). A more heterogeneous system with more stations at lower temperatures (or alternatively additional sampling later in fall when temperatures were lower) would have allowed for a more general representation of settlement at low temperatures. As such, caution is needed in applying this particular model to other systems that differ substantially from the parameter space in which the model was developed or those with substantial un-modeled intra- or inter-annual variability. Also, my environmental data is based on a single sampling event, in early August. *Ciona* become reproductively active in this system in July, so my data reflects patterns of early recruitment. Since my predictions are based on a single sampling event I can only estimate the early recruitment patterns, and I am unable to estimate the response of *Ciona* recruitment to environmental patterns that may evolve later in the year. Future work could collect (or model) environmental and biological data across a longer time period to forecast monitoring programs later in the year, but our current data
reflects early recruitment patterns which should be the focus of monitoring whenever possible.

There is a strong possibility that temperature is actually acting as a proxy for another environmental feature. This is a problem when fitting correlative models like GLMs. The ten stations with the lowest temperatures on which I observed recruitment were all located in the eastern end of the bay. It is possible that another un-modeled factor, which co-varies with along-river distance, may contribute to low recruitment observed towards the easterly, colder water stations. For instance at small scales, flow speed can affect the recruitment of a number of invertebrates (Abelson and Denny 1997), and water velocity likely increase nearer the shallower eastern end of the bay during mid-tides. Likewise, circulation patterns could affect the retention or concentration in particular areas. Such hydrodynamic factors were not, however, considered in this study but could be important in both the dispersal and settlement behaviour of larvae (Havenhand and Svane 1991). However, hydrodynamics are not as easily measured as temperature and salinity, and comprehensive understanding generally requires that a system-specific circulation model be developed – a costly and time-consuming endeavour. Incorporation of such information would, however, help disentangle the potential environmental factors that underlie the
observed patterns. I have identified locations of higher predicted relative probability of detection and advise managers to target search effort in the areas but further work is needed to refine my model to design specific surveillance strategies.

Although I feel that I cannot reliably extrapolate to dramatically different systems, my data show a clear, statistically parsimonious influence of midrange temperatures. Application to St. Peter’s Bay revealed regions at an appropriate range and with appropriate temperature which should be targets for monitoring. The addition of the two influences produced complex patterns. The magnitude of the true improvement to overall detection may be exaggerated since my model predicts no recruitment below 18°C. This limitation is likely to have been a consequence of the training data rather than a real response, and I suggest that managers working in colder systems parameterize temperature response in a comparable system before using my techniques for monitoring in a wider variety of systems.

My work addresses the pressing need for efficient and reliable monitoring approaches (Bax et al. 2001; Fox et al. 2009) and provides a new framework for
capturing propagule dispersal and environmental preferences and to relate these findings to generation of management techniques. I highlight the utility of concentrating monitoring efforts on larvae of a target species early in its invasion history and show how, with a relatively small dataset on recruitment and the surrounding environment, it is possible to largely characterize the recruitment mechanics of a targeted marine invader, and how such knowledge can be used to design early monitoring strategies to effectively manage at-risk systems.

Acknowledgements

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References

Allouche, O., Steinitz, O., Rotem, D., Rosenfeld, A. & Kadmon, R. 2008


Tables

<table>
<thead>
<tr>
<th>Model</th>
<th>AIC</th>
<th>R²</th>
<th>p</th>
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<tr>
<td>GLM-TS+D</td>
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<td>0.60</td>
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<td>BinomPWTSD</td>
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<td>0.62</td>
<td>0.36</td>
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</table>

Table 1.1: Comparison of four models of recruitment applied to Boughton River data. GLM-TS is the traditional generalized linear model (GLM) with just temperature and salinity, GLM-TS+D also adds mean distance to adult sources, ProbWeibTSD is the joint model with temperature, salinity, and mean distance to adult sources, using a negative binomial error function, and BinomPWTSD is the same as ProbWeibTSD but with a binomial error function. Columns show Akaike’s Information Criterion (AIC), coefficient of determination (R²), and the p-value for the Moran’s I statistic (p).
<table>
<thead>
<tr>
<th>Parameter</th>
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<th>Meaning</th>
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<td>$\theta$</td>
<td>5.98</td>
<td>1.78</td>
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Table 1.2: The best fitting parameters of my joint model resulting from fitting equation 1.3. Also given are the standard error and biological meaning of each term.
Figure 1.1: A map of the north-eastern portion of North America with detailed inset of Prince Edward Island, Canada. Below, detailed inset of the two study regions: St. Peter’s Bay (a) and Boughton River (b). Figure a maps the locations of the adult sources (triangles) and detection stations (circles). Figure b maps the locations of temperature surveys.
Figure 1.2: Predicted versus observed plots for the four models applied to field data of *Ciona intestinalis* (L.) recruitment in Boughton River. Panel a) show results from temperature and salinity generalized linear model, b) the results from the generalized linear model with temperature and distance (salinity dropped by model selection), c) the results of my correlo-mechanistic model with temperature
and distance and negative binomial error, and d) as c) but with binomial error distribution.
Figure 1.3: The modeled temperature tolerance and recorded recruitment for *Ciona intestinalis* (L.) in Boughton River. The points show the temperature values at which recruitment data was collected, and the curve shows the temperature sensitivity based on model fit in equation 1.3.
Figure 1.4: The modeled dispersal kernel based on 2008 recruitment data from Boughton River. The points show the temperature values at which recruitment data was collected.
Figure 1.5: A map of the probability of detection of *Ciona intestinalis* (L.) in St. Peter’s Bay, Prince Edward Island, Canada. Probability is plotted on a natural log-scale. Subfigures a-h) show the results of probability of detection mapping from each of eight different proposed introduction sites. Subfigure i) shows the total of all introduction sites.
Linking statement 2

The first chapter made significant advances in modeling the dispersal of invasive species but none-the-less the statistical kernel function it used only approximates the net movement of larvae. The actual underlying process that governs movement of larvae in water is far more advanced and involves the interplay of biology and physical movement of water. The second chapter in this section aims to compare the new family of correl-mechanistic species distribution model introduced in this chapter with more mechanistic techniques that attempt to estimate the underlying biological and physical processes of larval movement, rather than approximating them statistically. Both statistical and mechanistic models have the same goal: to predict locations of larvae to inform monitoring, however the mechanistic form is highly sophisticated and requires funding, expertise, and advanced computing facilities whereas the statistical type can be built with widely available statistical packages. In spite of a dearth of testing of mechanistic models they have come to dominate the field of marine dispersal modeling and I feel that by explicitly comparing the two forms I may avail simpler techniques to achieve monitoring and save substantial resources.
Chapter 2

A comparison of statistical versus mechanistic models for dispersal simulation:

new alternative models for larval dispersal simulation.

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Abstract

Modelling dispersal has a long history in ecology and many models of various levels of sophistication have been developed over the years. Species distributions models (SDMs) are a popular form of statistical model to forecast species locations and recent developments have successfully included dispersal in these models. However, the de facto standard type of model for modeling marine dispersal remains hydrodynamic (ocean current) models. There has been little effort to validate these models in general because biological survey data of dispersal are rare and, when available, the type of biological data collected in surveys (recruitment) is not compatible with models that simulate only the movement of larvae since they do not account for post-settlement processes. The net effect is that many dispersal models are not validated. I present a framework to appropriately scale recruitment data when needed and demonstrate how such a framework can be used to compare among traditional SDMs, correlo-mechanistic SDMs that include dispersal, and hydrodynamic models (or any other dispersal model), despite inherent incompatibilities in their outputs. I use robust data of recruitment of a harmful invasive species, *Ciona*, in Eastern Canada to demonstrate how various models of dispersal compare. I suggest that in addition to encouraging better validation of dispersal models in marine systems my results offer alternative models, in the form of correlo-
mechanistic SDMs – against which more complex, complicated models can be compared to justify their development cost.
2.1 Introduction

Forecasting marine biological dispersal is an inherently interdisciplinary endeavour; it is a complex process involving interactions among numerous biological and physical processes (Guichard et al. 2004). As such, dispersal studies have, since their early inception, been great consumers of sophisticated models. Forecasting the movement of organisms in marine systems is valuable in basic biological studies as well as the design of habitat reserves (Cowen and Sponaugle 2009) and commercial fishing (Gaylord et al. 2005, Grosholz et al. 2010). Models can forecast the locations of adults and larvae of invaders and these forecasts can be used to concentrate monitoring efforts (Meentemeyer et al. 2008, Chapter 1). Numerous types of models are available: correlative models that match climate and species occurrence to forecast where species are most likely to occur (i.e., species distribution models; SDMs), statistical dispersal models that attempt to estimate the processes of species movement with statistical functions (i.e., dispersal kernels), and mechanistic models which model the processes themselves that move species through marine systems (i.e., hydrodynamic current models).

Each of these models has varying degrees of applicability, complexity and cost. SDMs have been successfully used to forecast locations of many species.
Guisan and Thuiller 2005, Richards et al. 2007); however, they are widely
criticised for ignoring dispersal – for not recognizing that organisms must be
transported to an area of suitable climate before establishing there (Dormann et
al. 2007, Franklin 2010). Statistical dispersal models that include habitat
suitability and dispersal have been developed as a response to these
shortcomings of SDMs and have shown promising results (Leung and Mandrak
2007, Chapter 1). This type of correlo-mechanistic SDM models habitat suitability
in the same way as SDMs, but also estimates dispersal as a statistical kernel
function. Models with statistical dispersal kernels have a long history in ecology
and been able to satisfactorily capture dispersal outcomes in numerous systems
(Levin et al. 2003, Jones et al. 2005, Almany et al. 2007, Edwards et al. 2007,
Fletcher et al. 2013, Collin et al. in press). Due to the statistical nature of
dispersal in these models they ignore the processes which lead to the patterns of
dispersal and simply estimate the outcome of these unknown processes.

Mechanistic models are developed to estimate these processes explicitly. In a
marine dispersal context these models mainly solve systems of differential
equations to estimate water movement and are applied to simulate the advection
of larvae by water currents.
Recently, there has been a surge in the use of mechanistic models in marine systems, and these models are quickly becoming the *de facto* standard to model dispersal in marine systems (Gallego 2011). These models have repeatedly shown an impressive ability to capture the bulk flow of water in marine systems (e.g., Lazure et al. 2009, Renner et al. 2009). Whereas this flow of water may generally move biological particles (e.g., larvae) at large scales, accurate hydrodynamic forecasting of dispersal in marine systems remains difficult (Grosholz 1996, Wonham and Lewis 2009, Delaney et al. 2012). Mechanistic models thus still suffer physical and biological shortcomings; mechanistic treatment of waves, biological structures like sea grass beds or corals, and fluid mixing in hydrodynamic models are imperfect (Carlson et al. 2010, Manca et al. 2012) and these shortcomings are worse at small scales (e.g., 1 km) (Monismith 2007, Fossette et al. 2012). Unfortunately for biological dispersal models, Shanks et al. (2003) found that a great deal of marine invertebrates and plants do disperse on the kilometer scale and that these are the same scales at which dispersal distances were poorly predicted by a hydrodynamic model (Shanks 2009). Many operational mechanistic models operate under the exact conditions where poor performance should be expected.
Larvae are highly sensitive to a plethora of environmental stimuli, including light (Thorson 1964), turbulence (Abelson and Denny 1997, Fuchs et al. 2004), temperature (Anger 1991), salinity (Johnson and Katavic 1986), and even sound (Radford et al. 2007). These behaviors influence dispersal in two basic ways: i) species can move in the water column (usually vertically) in response to stimuli thus varying the flow regime they encounter and ii) larvae may respond to external stimuli by “choosing” to settle and surviving with greater probability in an environment with suitable conditions. Models ignore these biological influences at their peril; a recent study found that model sensitivity to biological parameters completely overwhelmed the influence of currents on dispersal (Paris et al. 2007). In general, biological responses are estimated from laboratory studies and are available only for a small number of species and are rarely sufficient to incorporate into hydrodynamic models applied to real-world systems. When biological information is lacking it is commonplace to make simplified assumptions about biological behavior (Roughan et al. 2011), which often leads to poor performance (Leis 2007, Delaney et al. 2012). In modeling studies larval duration time and release time are frequently cited as two important parameters (Forward 1987, Shanks et al. 2003, Fan et al. 2006), but many of these same studies exclude other forms of larval behavior.
Just as the poor model performance can be attributed, in part, to lack of biological data, so too can the lack of validation of these types of models. Foremost, robust data on the movement of marine larvae is rare (Eble et al. 2011, Berumen et al. 2012), but also the type of data collected is not comparable to the data produced by many models. Larval ecologists wish to know the precise movement of larvae, but are limited practically to surveying their final resting points. Such final resting points are the outcome of a series of steps beginning with larval supply from hydrodynamic and biological transport. Prior to being counted in a recruitment survey, larvae must arriving at a location (i.e., disperse there), “choose” to settle in an agreeable location and survive post-settlement predation and environmental stress before finally recruiting (Keough and Downes 1982). In the vast majority of dispersal studies only the final pattern resulting from the outcome of all steps is collected. In some studies this pattern correlates adequately with larval supply (Gaines et al. 1985, Jeffery and Underwood 2000) and in others it does not (McGee and Targett 1989, Jenkins 2005, Crean et al. 2010). Even if a hydrodynamic model can perfectly capture the physics of a marine system and larval movement in it, its predictions will be of dispersal, not recruitment – and comparing the models output to observed recruitment is inappropriate (Metaxas and Saunders 2009).
Due to the incompatibility of these data, few hydrodynamic dispersal studies to date have been able to present what is considered fundamental in other studies – an $R^2$ coefficient of determination indicating the amount of variation in observed recruitment explained by the dispersal model (but see: Broekhuizen et al. 2011, Delaney et al. 2012, Salama et al. 2013). Where models are compared, dispersal is often taken as a proxy for recruitment (Broitman et al. 2008, Pineda et al. 2010) even though the analogous practice of taking environmental data as a proxy for recruitment has been criticized in the SDM literature for a decade (Elith and Leathwick 2009, Wiens et al. 2009). Where data have been collected, it has been found that hydrodynamic dispersal models were unable to capture the biological recruitment patterns (e.g., Delaney et al. 2012). In spite of shortcomings in hydrodynamic models of dispersal, the spread of invasive species and the demand to design marine reserves has tempted researchers to use hydrodynamic models without validating their biology and occasionally presuming their accuracy (Inglis et al. 2006, Hinckley et al. 2009, Cetina-Heredia and Connolly 2011, Golbuu et al. 2012, Guizien et al. 2012, Elsäßer et al. 2013).

I feel that in light of the questionable performance of mechanistic models to simulate biological dispersal and the high cost of their development alternative models should be introduced to challenge these mechanistic models. Alternative
models are used widely in other fields of ecology to justify the use of a more advanced model over simple (but non-trivial) alternatives. If biological patterns can be adequately captured by simpler statistical models then management challenges can be addressed quicker and at a far lower cost using ubiquitous statistical software. Such a finding could save substantial development costs and could avail dispersal modeling to a larger audience by way of familiar statistical packages rather than highly specialized oceanographic tools. Before this can be achieved, the outputs of the various models must be made to have the same unit that is measured in biological surveys – recruitment – and researchers must agree upon some usable alternative models. I feel that the scientific community will benefit from a framework to do so (sensu Stow et al. 2009) and present a candidate framework to appropriately scale larval supply and compare dispersal models. I demonstrate how the results of traditional SDMs, advanced dispersal-aware SDMs (correlo-mechanistic; Chapter 1), and hydrodynamic dispersal models can all be compared to biological survey data and offer a coherent framework for researchers to do this in the future. SDMs have acknowledged limitations, especially in their ability to extrapolate to new environments (Franklin 2010) but my framework allows comparison of mechanistic models or any other form of dispersal model that may be more amenable to extrapolation, in addition to SDMs.
My case study is a relatively common situation where knowledge of dispersal is important to monitor for, and ultimately control an invasive marine species. As is often the case, especially following recent introductions of invasive species, there are limited data available about the larval behavior of the species, and these factors cannot be fully incorporated into the model. The biological data collected are typically recruitment data which is not consistently correlated to larval supply, and thus is not reliably comparable to the output of hydrodynamic dispersal models so direct validation is not possible. The species of interest is *Ciona* – a cosmopolitan species that has proven problematic and costly for mussel farming industries in eastern Canada (Howes et al. 2007, Ramsay et al. 2008), by fouling the crop and associated infrastructure. The harm this species causes in local bays, and the rate at which it has already spread has stoked substantial concern about its continued spread. Past studies facing similar challenges have used untested biological forecasts to make real management decisions (Huret et al. 2007, Moreno Navas et al. 2011). I subject this practice to scrutiny by comparing the ability of several models to capture recruitment patterns while also highlighting the need for model validation, and demonstrating a framework to do so.
2.2 Methods

2.2.1 Model system, species and data

I used recruitment data (Collin et al. in press) of *Ciona* in Boughton River, PEI. *Ciona* disperses via a short planktonic stage but possesses a short generation time so it can quickly dominate a bay. *Ciona* was introduced to a single bay in 2004, but has quickly spread and currently inhabits many bays throughout the province. Collin and colleagues conducted surveys of the adult distribution (33 transects) and the pattern of larval recruitment (82 stations) within Boughton River, a small, 6 km-long, semi-enclosed estuary on the eastern coast of PEI. Several mussel farms (and associated buoys and ropes) in the estuary provide habitat for *Ciona*. Temperature and salinity data were collected in conjunction with the recruitment data using a SeaCAT CTD at 2-m depth, the depth at which the settlement plates were deployed. This rich set of larval recruitment data allows for robust comparison among my models – two of which are fit statistical dispersal models and another with externally forced dispersal via currents.

2.2.2 Models

Recruitment is a two-step process: larvae must be transported to a site and must find the conditions there suitable for recruitment. The probability of a larva recruiting is a function of environmental conditions at the location where it
arrives. The larval supply to a site can be modeled using a statistical or mechanistic model, but the recruitment at that site will always be some fraction of supply, so supply must be scaled in all models so they may be compared to observed recruitment. Using this framework I can compare several models of transport, always appropriately scaling the number of arrivals by the environmental suitability they find, to equal an estimate of recruitment. This will allow us to scale transport fairly for all models and compare a suite of transport models on a level playing field.

I use the following equation to model recruitment,

\[ E(S_i) = (\beta_0 P_i + \beta_1) \frac{e^{\beta_2 T_i + \beta_3 T_i^2}}{\sum e^{\beta_2 T_i + \beta_3 T_i^2}} \]

where \( E(S_i) \) is the expected recruitment at site \( i \), \( P_i \) is the transport of larvae to site \( i \) (propagule pressure), \( T_i \) is the temperature at site \( i \), and \( \beta_{0-3} \) are fit coefficients. The first term on the right hand side of equation 2.1, in parentheses, scales the transport of larvae estimated by a given model and the second term fits the probability of recruitment as a function of temperature at the site (here I only consider temperature, as salinity was found not to be important for \textit{Ciona} recruitment (Chapter 1) (but a vector of environmental conditions with appropriate coefficients could be used instead). The first term scales the estimated transport in a linear manner (with slope and intercept) and allows
values of zero to be fit. The second term fits probability of recruitment as a parabolic function of temperature and keeps the probability bounded between zero and one. When the probability of recruitment is multiplied by the larval arrival the result is the expected recruitment at that site. This equation can be fit via maximum likelihood using input observations of recruitment and temperature and the output of a larval transport model (i.e., with one model fit to data, and one simulated from physical first principles).

I compared three models of larval transport by inputting their estimated values of $P_i$ (for all $i$) and re-fitting equation 2.1. The first, called “sdm,” does not include variation in larval transport ($P=0$, for all $i$), in which case the above model reduces to a standard species distribution model (SDM) using just temperature values and a constant value for larval supply ($\beta_1$) to predict recruitment. The second, called “joint,” is a statistical dispersal model using a fit Weibull function to estimate dispersal (sensu Collin et al. in press). This model includes distance information and two additional fit parameters,

$$P_i = \text{Wei}(\overline{D}_i; k, \lambda)$$

2.2

The distance, $\overline{D}_i$, is the average distance this location is to all adult sources, and $k$ and $\lambda$ are the shape and scale parameters of the Weibull distribution, respectively. Including both dispersal and temperature responses makes this
model one of a powerful new class of SDM that jointly models dispersal and environmental influence on recruitment processes to predict species distribution (Leung and Mandrak 2007, Chapter 1).

Finally, I use a hydrodynamic model in which the transport of larvae is driven by water movement as a result of wind, tides, and friction ("hydro"). It was forced externally by tidal outputs from the model of Chassé and Miller (2010). I selected the FVCOM model of Chen et al. (2003) as it is considered an advanced model that has been used for many recent biological applications (e.g., Gilbert et al. 2010, Stegert et al. 2012). This model a hybrid finite element-finite difference model in 3D, filling the bay with irregularly sized cells of varying sizes and mathematically estimates the flow of water among them; the model automatically tracks dynamic estimations of eddy diffusion within each cell.

Using the hydrodynamic model I simulated advection for these two weeks starting Aug 8, 2008, just as was done in the Boughton River experiment. Each of the 10 adult populations (Figure 2.1: triangles) were programmed to release 150 larvae every day (1500 total larvae per day, 2100 larvae per population over the two-week period) and their movement was estimated by the model. Each larva moved passively until the competency time, $t_c$, had elapsed after which time
if the larva moved within 3m of a station is would adhere to that station. Because I was only modeling 150 larvae released (likely by two orders of magnitude less than reality) smaller values of this distance threshold resulted in zero recruitment, so this buffer was used to ensure recruitment without biasing the location of recruitment more than 3m. If the larva had not settled after the larval duration time, $t_d$, had elapsed the larva (now aged $t_c + t_d$), was removed from the system.

2.2.3 Biological parameters

The hydrodynamic model required specification of two biological parameters: larval duration and competency time. These parameters have been found to be highly variable (depending on surrounding environment) and are not fully known for *Ciona*. Using available literature on *Ciona* larvae, I estimated suitable ranges and fit these parameters in the models. *Ciona* have lecithotrophic (non-feeding) planktonic larvae, which results in a relatively short planktonic duration (Dybern 1965, Svane and Havenhand 1993). Estimates for larval planktonic duration for *Ciona* range from 17.5 hours Hotta et al. (2007) to 24 hours Berrill (1947), in temperatures ranging from 16-20 °C. In addition to this, *Ciona* is an external fertilizers and Cirino et al. (2002) estimated that embryogenesis requires 18 h at 18-20 °C, and the duration of the subsequent competent period has been estimated to vary from 24-36 h at 18-20 °C (Dybern 1965). The higher water
temperatures encountered in Boughton River should accelerate the development of *Ciona*, and thus I use a range of 12-24 hours for embryogenesis in 12-24 hours for the competent larval period, leading to a total time of 24-48 h in the water column.

It has been well documented that *Ciona* spawning is triggered by sunrise (Castle 1896, Conklin 1905, Berrill 1947, Lambert and Brandt 1967), with gamete release normally occurring within 27 minutes of dawn Lambert and Brandt (1967). *Ciona* fertilize externally, and the gametes released are not immediately fertile. In my model I presume *Ciona* are released shortly after 06:00. Light also plays an important role during settlement and it has been previously found that settlement rates are an order of magnitude higher during daylight hours than at night (Collin *unpubl. data*). Therefore, I modelled a settlement time between 6am and 6pm. Since suitable settlement time (6am) is 24 hours after release time (6am), larvae that become competent in less than 24 hours will not be able to settle immediately. This parameter only affects the total larval duration; nevertheless I modeled the two stages independently for biological generality.

### 2.2.4 Fitting
The “sdm” model was fit using maximum likelihood and only fit $\beta_{1-3}$ from equation 2.1 (an intercept value for larval transport and the two temperature coefficients).

The “joint” model simultaneously fit the Weibull parameters, $k$ and $\lambda$, and the $\beta_{0-3}$ parameters including the temperature coefficients, all using maximum likelihood. The hydrodynamic model fit $\beta_{0-3}$, but instead of Weibull dispersal parameters the hydrodynamic model was allowed to fit $t_c$ and $t_d$, the biological parameters. Fits of $t_c$ and $t_d$ were discretized to one-hour precision due to the high computational demands of fitting a full hydrodynamic model. All models used maximum likelihood so they could be compared by Akaike information criterion (AIC) – allowing for selection of the best model of dispersal. All models presumed a negative binomial error structure for recruitment, as is recommended for biological count data (Zuur et al. 2009).

### 2.2.5 Comparisons

To compare the three models, I examined the spatial auto-correlation in the residuals of the observed and predicted recruitment from each model (and the auto-correlation of the data themselves) at four scales. Auto-correlation present in the data, but not present in the model residuals would indicate the model had properly accommodated the spatial structure of the data (Wagner and Fortin 2005). Additionally, I compared the coefficient of determination ($R^2$) of the
recruitment predicted by each model to the observed recruitment. Values near unity indicate the model was able to capture the recruitment patterns upon which it was built; the values also indicate the proportion of variation in recruitment explained by the model. I also present the AIC values of each model – values differing by more than two (i.e., ΔAIC>2) are considered substantially different (Burnham and Anderson 2002), and the model with the lowest AIC value overall is the most parsimonious. I calculated local Getis $G$ values for the predicted recruitment from each model. Local $G$ is an indication of the degree of clustering among the (three – in my case) nearest values (Getis and Ord 1996). Stations with a high $G$ value indicate hotspots of recruitment. To compare the predicted clustering of the three models I regressed the $G$ values of their predicted recruitment to the $G$ values of the real recruitment data. Models with local $G$ values highly correlated to the values of the data are accurately capturing the spatial clustering present in the data.

2.3 Results

Maps of predicted settlement (Figure 2.1) indicate that all models captured the bulk of the recruitment patterns, indicating greatest recruitment to the center-west of the bay, with little recruitment in the center. All models had inaccuracies in their predictions (Figure 2.2,1b-d) versus the observed data (Figure 2.1a), with
perhaps the *sdm* model (Figure 2.1b) performing worst, visually. All models were able to dampen the spatial auto-correlation in their residuals relative to the spatial auto-correlation present in the data (Figure 2.2). The *joint* model explained all spatial auto-correlation in the data and had no significant spatial auto-correlation at any distances classes. The *sdm* and *hydro* models had significant spatial auto-correlation at mid-range distances.

Table 2.1 shows that the most parsimonious fitting model is the *joint* model with AIC=404.2 and $R^2=0.61$. This model was far better ($\Delta$AIC>>2) than either the *sdm* or *hydro* models which had AIC values of 454.4 and 451.5 respectively and common $R^2$ values of 0.42. The models also showed similar results when compared by the correlation of their local $G$ values. The *sdm* and *hydro* models had similar $G$-value $R^2$ (0.57 and 0.58, respectively) and the *joint* model was higher ($R^2=0.80$). The correlation plots in Figure 2.3 show that all the models predicted the observed recruitment fairly accurately, explaining between 42% and 61% of the variation in recruitment. All models predicted zero recruitment at locations where more than zero was observed (stacked points near the origin of each plot). The joint model (Figure 2.3b) predicted recruitment most accurately.
The hydro had the best fit with a larval competency time of 24 hours and a duration time of 19 hours (43 hours total). The models all fit probability of recruitment curves for temperature, and the sdm and hydro models fit nearly identical curves with peaks near 23 °C (Figure 2.4). The joint model fit a different curve with a slightly higher peak than those of the other two curves (Figure 2.4).

The hydrodynamic model advected larvae in a seemingly realistic manner, carrying larvae along current jets that followed the shape of the bay and flushed larvae in and out with the tidal cycle. I show an example of some larval paths advected by the hydro model in Figure 2.5. The larval transport estimated by the hydrodynamic model (prior to being scaled by recruitment probability) bore almost no resemblance to the observed recruitment pattern, explaining only 3% of the variation in observed recruitment ($R^2=0.03$; $p>0.05$). This is likely why the SDM model with only scalar dispersal was able to perform as well as the hydro model.

2.4 Discussion

My work clearly shows that comparisons of dispersal models are a justified and necessary exercise. I compared models using a rich set of recruitment data, and I demonstrate how to properly scale the larval transport in these or any model by
fitting a probabilistic recruitment model so model outputs can be compared to recruitment data. I introduce a new standard of alternative models for dispersal model comparisons which themselves show promising ability to predict dispersal. The hydrodynamic model used in this study is a cutting-edge model, but was not able to capture recruitment any better than a simple statistical SDM. The common practice of using un-validated models with approximate biology can give misleading results. In part due to their incomparability with biological survey data, many of the models are un-validated (Stow et al. 2009) and validation status has no influence on the citation rate of these papers (Arhonditsis et al. 2006). Furthermore, the practice of assuming larval transport data is a suitable proxy for recruitment data can also give misleading results.

Biological data to assess dispersal models are rare (Berumen et al. 2012) and I demonstrate here how valuable and necessary such data are. Even when available, the use of such data to evaluate dispersal models has been hampered by incomparability with model outputs. I demonstrate how recruitment data collected as part of these types of projects can be compared to tracking models outputs in a more robust way. This should facilitate future evaluation of dispersal models and help answer numerous calls for better model validations (Cowen and Sponaugle 2009, Haase et al. 2012). I suggest that advanced hydrodynamic
models may not always be necessary for these applications. Statistical models may suffice, or where they do not suffice they may be used to justify the expenditure on a more advanced hydrodynamic model. I show how the data needed to generate a hydrodynamic model are more than enough to also generate several types of alternative models. SDM models like the ones I demonstrate have been used to guide management efforts in numerous systems (Huret et al. 2007, Moreno Navas et al. 2011) and may be promising as alternatives to complex hydrodynamic models, especially where oceanographic expertise within a research unit, money, or supercomputing facilities are limited – however, caution is still warranted when trying to extrapolate to new systems.

The hydrodynamic model (hydro) had access to all data available to the other models: adult locations, and temperature data, as well as some additional data not available to the alternatives: salinity, tide, time, and the 3D shape of the bay but seemed less able to use these data to capture the observed patterns of recruitment. Somewhat surprisingly, an increase in data available to this model was not matched by an improved ability to capture recruitment patterns. The predictions from the hydrodynamic model were not grossly inaccurate; it was able to capture the general pattern of recruitment, but this was due primarily to the fitted environmental variables. Imprecision in these predictions could be
interpreted as a failure of the FVCOM model to capture the water movement of Boughton River, but it could equally be a failure of the biological features included or in the parameterization of the FVCOM model itself, which required substantial additional inputs of physical data. This suggests that other post-settlement processes may be dominant instead of transport. I do not dismiss the power of hydrodynamic models, but their ability to incorporate biological factors should not be presumed – this study is meant as a demonstration of that. Since hydrodynamic models generally struggle to model smaller scale systems, I suspect that my case study may be an example of one of the harder cases for such models. Boughton River is small and is not a subsection of a larger system with predictable, large-scale dynamics, which may make it harder to model than other small-scale systems. *Ciona* has short-lived larvae meaning that they do not survive for long and do not travel far. The exact behavior and environmental response around their movement and settlement out of the water column also requires exploration. Such short temporal scales may be harder to capture than long term movement since they can be more sensitive to small errors. I am unable to draw specific conclusions as to why this hydrodynamic model performed poorly, but I suspect it is a combination of an incomplete understanding of the larval behaviour of *Ciona* during dispersal and settlement, the small size of Boughton River, and the short timeframe that I was modelling.
Recent advances in SDMs avail powerful models to answer questions of biological dispersal in marine systems (Leung and Mandrak 2007, Chapter 1). These models simultaneously fit a dispersal kernel and an environmental tolerance for a target species. In many ecological studies these are the most important elements of the study and all the details of the hydrodynamic model like halocline, thermocline and water level throughout the bay are of unnecessary consequence. Moreover, these models are simple to use and can be developed with standard statistical software. This advantage, in combination with their apparent ability to capture biological patterns, should challenge biologists developing advanced hydrodynamic models to consider the value of deploying statistical models, at least for comparison purposes. It would appear that the SDM approach presented here and adapted from Chapter 1 has promising ability for use in this application.

By design, I included only a minimum of biological parameters in my model – I only fit two. Duration time and release time are frequently cited as two important parameters (Forward 1987, Shanks et al. 2003, Fan et al. 2006), but others are suspected for this species. For example, *Ciona* can swim (Chia et al. 1984) – perhaps in response to variations in light levels as with other ascidians (Young
and Chia 1985). Fitting any more parameters would be computationally costly; I spent 6500 CPU-hours fitting just two parameters. Other species whose biology is better understood may require less fitting, hence the need for biological data before attempting to model a species mechanically. Larval ecology is complex, and evidence is mounting that until it is better understood, our most advanced hydrodynamic models may offer little in terms of performance improvement. I hesitate to suggest that the values I fit for competency time \( t_c \) or duration time \( t_d \) are accurate estimates of the larval ecology of *Ciona* since the hydrodynamic model that used those values performed questionably. Due to the restrictions placed on timing of gamete release (sunrise) and settlement (only in daylight), larval competencies \( \leq 24 \) hours are all equivalent, so the model was likely biased to select 24 h. Perhaps these parameters are not as important as I expected them to be.

Forecasting of larval dispersal is very important, and I suggest for future consideration, more traditional statistical models are used before additional time and money is invested in advanced mechanistic models, to ensure that the additional effort required is beneficial. I implore other researchers to rigorously validate their dispersal models and encourage them to compare their physical models to statistical ones. Ensuring model validation becomes common practice
will lead to more reliable biological predictions and better management of marine ecosystems, and perhaps many cases of accelerated, less expensive dispersal research.

Acknowledgements

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References


Crean, A. J., S. E. Swearer, and H. M. Patterson. 2010. Larval supply is a good predictor of recruitment in endemic but not non-endemic fish populations at a high latitude coral reef. Coral Reefs 29:137-143.


Edwards, K., J. Hare, F. Werner, and H. Seim. 2007. Using 2-dimensional dispersal kernels to identify the dominant influences on larval dispersal on continental shelves. Marine Ecology Progress Series 352:77-87.


Tables

<table>
<thead>
<tr>
<th>Model</th>
<th>$R^2$</th>
<th>AIC</th>
<th>Local G $R^2$</th>
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<td>0.57</td>
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<td>404.2</td>
<td>0.80</td>
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<td>hydro</td>
<td>0.42</td>
<td>451.5</td>
<td>0.58</td>
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Table 2.1: The comparisons of the three different models used. The table shows three metrics of comparison: coefficient of determination ($R^2$), Akaike Information Criterion (AIC), and local Getis coefficient of determination (local G $R^2$).
<table>
<thead>
<tr>
<th>Parameter</th>
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<th>joint</th>
<th>hydro</th>
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</thead>
<tbody>
<tr>
<td>$\beta_0$</td>
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<td>648.2</td>
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<tr>
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<td>27.7</td>
</tr>
<tr>
<td>$\beta_3$</td>
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<td>-0.15</td>
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<td>$k$</td>
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<td>N/A</td>
</tr>
<tr>
<td>$\lambda$</td>
<td>N/A</td>
<td>1.78</td>
<td>N/A</td>
</tr>
</tbody>
</table>

Table 2.2: The best fitting parameters for each model from equation 2.1.
Figure 2.1: Maps showing actual and predicted recruitment at each station in Boughton River: (a – top left) observed data; (b – top right) “sdm” model, (c – bottom left) “joint” model; and (d – bottom right) “hydro” model.
Figure 2.2: Correlogram showing the degree of spatial auto-correlation (as measured by Moran’s $I$) at various distance classes. The “data” line shows the spatial auto-correlation in the recruitment data, the other lines show the spatial auto-correlation in the residuals of the models.
Figure 2.3: Correlation plots showing predicted and observed recruitment from each model: (a) sdm; (b) joint; and (c) hydro.
Figure 2.4: The fit temperature response curves for the models with temperature parameters.
Figure 2.5: An example of the paths taken by the larvae as advected by the

*hydro* model. The black dots represent the locations of larval release points and
the grey squares the locations of detection stations.
**Linking statement 3**

The first section of my thesis concerned the optimal detection of marine invasive species. It develops sophisticated models to guide monitoring programs in marine environments. It compares these models to other, more popular, but sophisticated models to help advise managers on which model may be appropriate in their system. To a manager facing a marine invasion, monitoring can be just the first step. Following a successful detection of an invader steps can be taken to prevent that species from causing harm. There are many forms of control available, but the only one that can completely prevent harm is eradication – the complete removal of the invader. Eradication is often a desired control target, but is rarely achieved in practice, in part because there is a lack of quantitative frameworks to structure an eradication program or to gauge its feasibility of success, and thus reluctance on behalf of managers to initiate an eradication campaign. The second section of my thesis develops and applied quantitative frameworks for eradication. Chapter 3 argues that eradication is not always adequately considered, and I develop a framework for rapid assessment of its feasibility. This quantitative model offers criteria to rapidly assess the potential for eradication and provides estimates of the necessary effort and timing, and of the size of the target area. This framework is applied to the same tunicate invasion that Chapter 3 designed monitoring programs for,
demonstrating a complete invasion management program of monitoring and eradication of this tunicate, and possibly other marine invaders. My framework suggests that eradication may be feasible and, due to a low cost of eradication versus the benefit, could require only a 16% chance of success to constitute a worthwhile risk (since costs are 16% of the benefits).
Chapter 3

Re-evaluating eradication of nuisance species: Invasion of the tunicate, *Ciona intestinalis*.

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Abstract

Eradication is an eminent concept in the management of biological invasions but is rarely considered in practice. This may occur because managers commonly face incomplete data and a lack of practical guidance. Past eradication frameworks provide useful heuristics, but do not provide quantitative guidelines. I argue that eradication is not always adequately considered, and develop a framework for rapid assessment of its feasibility, despite limited data. This quantitative model offers criteria to rapidly assess the potential for eradication, as well as provides estimates of the required effort, timing, and target area. This framework is applied to a recent tunicate (*Ciona intestinalis*) invasion in Prince Edward Island (PEI), Canada, which is causing considerable economic damage to harvesters of blue mussels (*Mytilus edulis*). My framework suggests that eradication may be feasible and, based on a cost-benefit analysis, requires only a ≥16 percent chance of success to be a worthwhile risk.

3.1 Introduction

Many non-native tunicate species have recently invaded coastal waters of North America and pose significant threats to marine ecosystems (McKindsey et al. 2007). They occur in such massive numbers that the substratum itself may be entirely obscured (Figure 3.1). Particularly, the invasion by the tunicate *Ciona* is
considered at a “crisis level”, and is a major marine invasive species issue for the Department of Fisheries and Oceans Canada (DFO) (DFO 2007). The species has a remarkably high fecundity and reproductive rate (Gray and Christie 1983), often with several generations present in a single season (Svane and Young 1989). *Ciona* is thought to have been introduced to PEI by the bivalve aquaculture trade (Lambert and Lambert 1998). It broadcast spawns; freely releasing gametes into the water column; but its inter-bay transfer seems minimal suggesting that spread between bays is via infrequent, human-mediated transport. In Prince Edward Island (PEI), Canada, *Ciona* has spread from first detection in 2004 to smothering densities in several bays in 2007. *Ciona* blankets aquaculture crops, threatening the mussel-farming industry, putting 77% of Canada’s mussel farming in danger (DFO 2006). At a more human level, mussel farmers who have spent decades developing their farms are losing their livelihoods (T Landry, pers. comm.).

Despite the social relevance of *Ciona*, current managerial guidance is insufficient to control *Ciona*. This may be because information on population biology rarely exists early in an invasion, which has been used to justify inaction (Simberloff 2003). As a result, an invader will often have major impacts before action is taken (Mack et al. 2000). To minimize such impacts, managers need to increase their
rate of response, despite uncertainty and limited information (i.e., the precautionary principle; Kriebel et al. 2001). This may be possible as only a subset of data is typically required to assess the feasibility of a given management option (Roe 1998, Simberloff 2003). Herein, I identify the information required to assess the possibility for eradication of invasive species.

Eradication is a major idea in invasion biology and is often an explicit goal of government (Genovesi and Shine 2004). However, there are few examples (see Mack et al. 2000 for a review), especially in marine systems (but see Culver and Kuris 2000, Bax et al. 2001, Miller et al. 2004, Wotton et al. 2004, Anderson 2005, Hopkins et al. 2011). The few marine successes have typically occurred in the early stages of invasions; after establishment and initial spread, eradication is typically no longer considered. For Ciona, in particular, eradication has been considered virtually impossible, given their astonishing population growth rates and spread. I disagree and propose that it may be feasible to eradicate Ciona and other established invaders, and that this should be assessed explicitly.

I argue that eradication has been prematurely dismissed in practice due the lack of practical, quantitative steps for management. The papers that have examined this important issue have provided general heuristics regarding eradication
success [e.g., it is early in an invasion (Simberloff 2003); the species has biological characteristics susceptible to control (Myers et al. 2000); rates of removal are greater than rates of reproduction (Bomford and O'Brien 1995); see also Appendix B]. While these heuristics are useful, and the Ciona invasion meets many of their requirements, they provide little instruction on the more practical elements of eradication that are of most interest to managers such as cost, scope, and time and research required. Such explicit frameworks need to be developed to fully evaluate the potential for eradication and to provide managers these useful parameters. In this chapter, I develop this general, quantitative framework for eradication, and identify the few key biological parameters that are required. Finally, I apply the framework to a case study of Ciona.

3.2 Model

In formulating a conceptual model, I reduce complexity to five self-evident general core statements: 1) simply put, invaders get to new places and grow; 2) locations can become (re-)infested from other invaded locations, limited by dispersal; 3) growth of populations follows life cycles, from larval or egg stage, to non-reproductive juveniles, to reproductive adults, which in turn produce more larvae (Figure 3.2); 4) if we can disrupt the system, we can stop reproducing
adults from forming, and the population will eventually go extinct; 5) some stages may be more susceptible to management actions than others (Buhle et al. 2005). My analysis of eradication follows from these statements.

To disrupt the cycle, I define a vulnerability “time window” \( (t_w) \) as a minimum range of susceptible, pre-reproductive ages of individuals (e.g., growth to a visible size or immobility below a certain age) (Figure 3.2). Of course, reproductive individuals should be killed if possible. However, the crucial factor is that a subset of pre-reproductive stages can be eradicated, since this will stop reproductive individuals from forming.

Next, I determine the number of passes (repeated treatments of sites) needed for eradication using the time window and the progress along life cycles (Figure 3.2). I conceptualize the process as a “ratchet effect”. As younger juveniles mature, they enter the vulnerability time window. Each time a pass is made all individuals within the window are removed. Thereafter, the life cycle ratchets – younger individuals missed by the previous pass mature and become vulnerable, to be removed in the subsequent pass. Since the time window starts before the age of maturity, and since individuals are kept from aging beyond the window, no new adults develop. Thus, via multiple passes on just a vulnerable stage, potential
sources of propagules can be removed from a population while existing adults are either removed directly or eventually experience natural mortality. The feasibility of this approach is improved because not all individuals need be eradicated at once – individuals outside the window can be unaffected. Further, as discussed below, not all populations need be treated simultaneously; rather “treatment zones” can be defined, focusing on fewer local populations.

Using knowledge of the vulnerability time window ($t_w$), which defines both the length of time that juveniles are vulnerable and the maximum time within which a pass must be made, I can define an important criterion for eradication success. Assuming that spread can occur among local populations, cleared areas can become re-infested by other invaded areas within the bay. Therefore, a manager must be able to finish treating relevant local populations before younger juveniles mature beyond the window, become reproductive, and act as continuing sources for the system;

$$t_w > Nt_i + t_i$$  \hspace{1cm} (3.1)

The total time for a pass is thus the treatment time of each population, $t_i$, multiplied by the number of local populations, $N$, plus an additional $t_i$ since time must be allotted to begin a second pass to treat the first population again. This
must be done before missed juveniles in this population mature beyond the window.

If treatment over the whole system is logistically infeasible, eradication may still be possible by sweeping over the system making overlapping treatments on a smaller area, which I term the “treatment zone”. Exchange of larvae among the populations within the treatment zone will be halted after sufficient passes. However, populations outside of the treatment zone will be freely growing and spreading. If the treatment zone is larger than the maximum spread distance within the time window, some populations within the treatment zone would be out of the range of larval influx from outside populations (Figure 3.3i: B-D). The next treatment zone (Figure 3.3ii) would overlap the re-infested populations (Figure 3.3i,ii: E,F), but some local populations would remain un-infested. This introduces the second eradication criterion: the size of the treatment zone must exceed spread within the time window.

The three components developed above – number of passes, time window, and treatment zone – provide the context for assessing the feasibility of eradication. This framework does not require in-depth analysis of many population dynamics parameters such as fecundity, recruitment, or carrying capacity. The consistent
critical information required to estimate two of the three components, number of
passes and time window, relate to maturation time. If, and only if, the entire
system cannot be treated within the time window, knowledge of spread is also
needed to estimate treatment zone. Additionally, if, and only if, adults cannot be
effectively removed, adult survivorship becomes relevant because we need to
know how long adults will continue producing new individuals. Nevertheless, my
framework dramatically reduces information requirements thereby allowing more
rapid management action.

As with any eradication effort, there is a chance that some individuals are
missed. To evaluate the success of the eradication effort, monitoring should
follow any eradication effort. Arguably, populations missed during the eradication
program should be limited to sparse nascent foci (Moody and Mack 1988, Mack
and Lonsdale 2002). Monitoring could focus continued eradication efforts to
these nascent populations and treat them locally, rather than restarting the entire
eradication program. Further, with smaller population sizes, processes such as
population and environmental stochasticity and Allee effects can result in the
extirpation of remaining individuals (Liebhold and Bascompte 2003).
3.3 Application to *Ciona intestinalis* in PEI.

*Ciona* is a major nuisance in PEI with high numbers of individuals, and high fecundity, making them appear, at first glance, to be impossible to eradicate. However, eradication may be possible and relatively little information is required to assess its feasibility. Potential eradication is aided by the fact that *Ciona* does not survive everywhere – it requires solid substrata, which in PEI primarily consists of man-made structures: docks, buoys, mussel farming infrastructure, and the mussels themselves. *Ciona* have been observed on rocks in their native range (Dybern 1965), but current evidence suggests that they should be very sparse or absent on rocks in PEI. There is virtually no natural surface available for settlement (Locke et al. 2007). The substrata are predominantly silt, mud, or sand (Cambell 1973, MacWilliams and Judson 1973, Murchison 1973), which are unsuitable for colonization.

At the local scale, eradication can be very effective. The removal of individuals can be conducted in one of three ways, depending on the type of surface targeted. First, vinegar is one hundred percent effective against *Ciona* after one minute of exposure (Carver et al. 2003). Second, air drying is also completely effective, and either of these methods could be used to clear any structure that can be removed from the water (e.g., mussel lines, buoys, small docks). Larvae
settling after returning the object to the water could be removed in a second pass. For these structures, the vulnerability time window would be the minimum maturation time, estimated at 45d (Liu et al. 2006).

Thirdly, all permanently-installed structures and any natural substrata found to support *Ciona* need to be treated manually, for instance, by hand or vacuuming (i.e., Coutts 2002). Removed individuals are unable to reattach and should die off quickly on the silt bottom. While requiring significantly more effort, this method is still highly effective (Pannel and Coutts 2007) against individuals above a visible size. Thus, the vulnerability time window would be from visible age, \( t_v \), to maturation age, \( t_m \). I assume a diver can see an individual 1.5 cm in length. From laboratory studies, this length is reached just after 25d (Liu et al. 2006) which is thus the visible age. The difference between this age and the maturation age (45d) leaves a time window, \( t_w \), of approximately 20d for manually-treated structures (docks and, if infested, rocks).

I have estimated the total cost of treating each of these surfaces, including mussel farming equipment, docks and rocks, as follows: *ca.* $1.1 million per pass for mussel farming infrastructure, *ca.* $561 000 per pass for docks and other man-made structures and *ca.* $380,000 per pass for rocks (Appendix 1).
If coordinated treatments could be completed on these surfaces within the time
window, recruitment would be stopped and the cycle would be disrupted. The
number of passes required for this to occur can be estimated for *Ciona* using the
following equation,

\[ P = CEIL \left( \frac{t_v + L + N t_t}{t_w - t_t} \right) + 1 \]

Where *CEIL* is a rounding-up function, *t_v* is the visible age, *L* is the maximum
larval duration, *N* is the number of populations treated, *t_t* is treatment time of a
local population (e.g., a single dock), and *t_w* is the duration of the time window.

For manual treatment, the first pass, represented by the “+1”, removes all *Ciona*
of visible size, including adults. Thus, after the first pass, larvae are no longer
produced and only non-visible juveniles and larvae remain (*t_v*+*L*). The *N t_t* term
expresses the time spent conducting the first pass, during which larvae would
continue to be generated, re-colonizing structures. At each additional pass,
juveniles that had grown to visible size would enter the window and could be
eradicated. Thus, I can determine the number of passes required by dividing the
surviving untreated stages – previously invisible ages, larvae, and individuals that
matured during treatment - by the window. *t_t* is included in the denominator of my
equation to account for the fact that individuals will age during treatment of a
local area. For treatment with vinegar or air, all attached individuals are killed,
and \( t_v \) would effectively equal zero. Given the equation, the length of the larval phase (1.5d), taking \( t_w \) to be the difference between visible age (25d) and mature age (45d), and assuming that each of the five infested bays has 12 small docks which can be treated in a day (\( t_t = 1d \)), I estimate four passes for manually-treated structures, and two for air- or vinegar-treated ones.

In summary, I believe that eradication may be possible, if treatments can occur within a time window of ca. 20d for manually treated structures (manmade and rocky structures) and ca. 45d for vinegar treated structures (mussel farming infrastructure). I provide guidance for research – the most important information needed to assess the feasibility of eradication relate to maturation time, which will dictate the time window. Further, I emphasize the importance of coordination and of multiple passes.

### 3.4 Benefit-Cost Ratio of Eradication

Since *Ciona* threatens the valuable mussel farming industry, the potential benefits of eradication are high. To estimate the economic benefits of eradication I estimated the discounted cost of current treatment efforts to be $28 million (at a 5% discount rate). At an estimated cost of $4.4 million my strategy has a benefit to cost ratio of 6.6:1 (see Appendix A for calculations). Put another way, an
eradication attempt would be economically worthwhile, even if there were only a ≥16% chance of success. This conservative estimate does not attempt to estimate potential reasons for eradication failure such as a lack of stakeholder participation, poor coordination of treatment. These cost-benefit estimates provide managers a lower bound for the total probability of failure, below which eradication would no longer be economically viable. If, however, *Ciona* were found to be appreciably present on natural structures, this ratio would become 1.7:1. If this were found to be true the decision about economic viability would be more difficult. The treatment costs for all the mussel-producing bays, however, would be approximately $4.9 million, and to prevent the potential spread to the other bays in PEI, effort now would have a 4.3:1 benefit to cost ratio.

3.5 Discussion

Currently, efforts to control *Ciona* are carried out at significant annual costs, and with no long-term benefits. These efforts have little long-term impact on *Ciona* populations, because management has been largely uncoordinated - individual mussel farmers treat their equipment, but do not synchronize with other farmers (T. Landry, pers comm.). Further, there has been no attempt to treat other structures such as docks. Though there are few docks, when untreated they still provide sources of new larvae. Scientists can aid society by framing the problem
such that potential solutions emerge. I have shown here how eradication could be realized with modifications to existing efforts.

Prior frameworks have developed valuable heuristics for considering eradication (e.g., Bomford and O'Brien 1995, Mack et al. 2000, Myers et al. 2000; see also Appendix B), but more quantitative guidance is needed. My efforts overlap several of these frameworks, highlighting the need for coordination, continued political will over the entire period of treatment, and the required susceptibility of the organism to treatment. In addition, I offer quantitative results – how many passes are required by how many people over what time frame and area, and at what cost. I illustrate that multiple passes are needed, even when population levels of the invader are not immediately causing ecological or economic harm. Further, my framework facilitates rapid assessment and response by focusing research: maturation time, and the associated vulnerability time window, is the most critical component for eradication feasibility. Once the infestation is delineated, I argue that eradication may be achieved even if only a fraction of pre-reproductive stages are treatable (the vulnerability time window and ratchet effect concepts) or the system is too large to be treated simultaneously (the treatment zone concept).
Of course, as with any eradication attempt, some individuals may be missed; to optimize any additional efforts needed to treat any surviving local populations, I recommend monitoring. Arguably, populations missed during the eradication program should be limited to sparse nascent foci (Moody and Mack 1988, Mack and Lonsdale 2002). Such small, isolated populations would be subject to processes such as population and environmental stochasticity and Allee effects which could result in the extirpation of remaining individuals (Liebhold and Bascompte 2003). Without much information on population dynamics, stochastic dynamics should not be relied upon. Following this and any other eradication effort, I recommend monitoring to assess success and, if needed, to focus continued treatments to these local populations. The specifics of such a monitoring scheme are beyond the scope of this paper.

Population viability analysis (PVA) has been employed in conservation to estimate the probability of a species going extinct. Of course, when treatment is totally effective, a transition probability from juvenile to adult is zero and survival is impossible. Sensitivity analyses (or the comparable elasticity analysis; Benton and Grant 1999) have been applied to these models and have identified certain life stages that, if targeted, have the greatest impact on growth rates (McEnvoy and Coombs 1999). Generally, for
rapidly increasing species with short life spans (like many invaders), juvenile survival is an efficient management target (Biek et al. 2002; Buhle et al. 2005). Therefore, there may be some merit to applying our treatment window concept even when treatment is less effective as this is still an efficient approach to eradication.

While I believe that eradication may well succeed for *Ciona*, the probability of success only needs to be 16% to be worthwhile based on cost-benefit analysis. This risk evaluation, in combination with the apparent feasibility of my strategy, certainly suggests that the eradication option has been prematurely dismissed and is worth consideration for *Ciona* in PEI. Further, I feel the framework can be sufficiently generalized to identify possible opportunities for eradication in many other systems. It was built from core concepts that apply to nearly any invasion. The heart of the framework, the vulnerable time window concept – a species having a particular pre-reproductive vulnerable stage – is applicable to many species. The framework was constructed to contend with the common problem of population data lacking for new invaders. This situation arises with many invaders, and the use of my framework may be a valuable diagnostic tool to formulate a solution.
While I presented an in depth analysis of my framework only for *Ciona* in PEI, I feel it has broad applicability. The framework is based on general character traits shared by many invaders and requires minimal information. The grey squirrel (*Sciurus carolinensis*) in Italy (Bertolino and Genovesi 2003), for example, seems to exhibit characteristics conducive to my method. It has a vulnerable stage before reproduction when it is confined to a large, visible nest. It is also well known that the squirrel remains in this stage for many weeks (Moore et al. 1997), during which treatment could occur. This stage could be targeted in many passes, and the adults would not have to be trapped or killed. Additionally, its delineation and rate of spread are well known (Bertolino and Genovesi 2003).

While the framework offers one conceptual avenue for eradication, others may be possible. I urge researchers to further develop a suite of general frameworks to fully identify the scenarios where eradication may be possible, and to quantitatively assess the feasibility and the conditions necessary to achieve eradication, using minimal population data. I continue this work myself in Chapter 4, but more research is still needed. Conversely, these frameworks can also clarify when I should expect eradication efforts to fail – e.g., if treatment cannot be completed within the time window or managers only attempt a single eradication pass, the cycle will likely remain unbroken and efforts will be
ineffectual. Similar frameworks should be developed for eradication and other components of an invasion management toolbox, such as control or prevention.

3.6 Conclusion

The framework provides practical, timely, quantitative guidance, estimating the characteristics of the strategy of most use to managers: cost, required number of workers, timing of treatments, spatial scope, and number of passes – all with very little population data. I demonstrated its power by taking an invasion once considered hopeless and showing how, seen from a new perspective, full eradication not only seems feasible, but may indeed be economically preferable. Thus, rather than the usual defeatist dismissal, eradication should be seriously considered and quantitatively analyzed. I hope this perspective will be cast on other invasions and that eradication will prove feasible where historically it has been considered impossible.

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References


Figure 3.1: Socks of blue mussels coated in *Ciona intestinalis*.
Figure 3.2: The generalized life cycle of an organism, showing each life stage (larvae, juveniles, adults) and the vulnerability time window. Radial axis represents relative numbers of individuals, and circumferential axis shows time. As the population matures, individuals enter the vulnerability time window. This window also defines the maximum time available for a treatment pass (Equation 1). With each additional treatment pass, the “ratchet” turns and an additional
portion of the life cycle becomes eradicated. With sufficient turns of the ratchet, the entire population can be extirpated.
Figure 3.3: The “treatment zone” concept over many populations: (a) at the initial time interval, populations B, C, and D are out of the range of spread from untreated sources; (b) at the second time interval, after treatment passes on populations B–F, populations B, C, and D (designated by X) are cleared, and the
treatment zone is moved to encompass new overlapping populations; A, E, and F are now out of range of spread from untreated sources. It may be possible to sweep through a system, eventually allowing full eradication, if the treatment zone exceeds the maximum dispersal distance, and if each pass across local populations within the treatment zone can be completed within the vulnerability time window (Equation 1).
Chapter 3 developed the first quantitative framework for eradication. This is the first framework to offer quantitative conditionals for eradication and specify the precise cost, scope, and required timing to achieve eradication. This framework was the first entirely quantitative framework, but (as highlighted in the chapter) there have been other frameworks with some quantitative (or partly quantitative) elements that still offer good guidance. In fact there are dozens of eradication frameworks that provide quantitative, qualitative, but sometime superfluous and contradictory advice. My goal in the final chapter of my thesis was to combine the advice of published eradication frameworks into a single framework and where possible to modify their guidelines to be more quantitative, more general, less contradictory, and to incorporate them into the most useable form – a decision tree. This tree assembles all the best advice from eradication frameworks and presents the best available tool for managers to make informed, scientific decision about when eradication may be feasible and how it should proceed. This builds on the framework in Chapter 3 by adding strict, multi-scale immigration rules, mobility considerations, and explicit consideration of spatio-temporal variability in treatment efficacy, plus guidance from over a decade of published eradication frameworks by other authors.
Chapter 4

A synthetic meta-framework to rapidly evaluate feasibility and cost of eradication of exotic species

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Abstract

Eradication remains a frequent ambition of invasive species management programs, but it is often difficult to achieve in practice. This is partly due to a lack of useful tools to evaluate feasibility of eradication and design a campaign. A diversity of eradication frameworks exist, wherein some 43 guidelines are outlined to achieve successful eradication, comprising ecological tests, heuristics, and best-practices. Despite this background, it is unclear how to apply these guidelines in practice, because they (a) often lack a quantitative and/or experimental basis to evaluate efficacy, (b) can be taxon or habitat-specific and may not apply to most invaders, (c) may offer prescriptions that are too vague to guide real eradication programs, (d) suggest research that is not always strictly required make decisions, or (e) occasionally disagree with one another. Here, I attempt to address some of these issues by distilling the most common prescriptions from across the many frameworks, converting existing guidelines to definite quantitative experiments and measures, and showing how the latter can be organized into a procedural decision tree to evaluate eradication. I formulate a meta-framework which offers quantitative tests of eradication feasibility, and where it does not dismiss eradication outright, it helps refine the operational parameters necessary to achieve it. I apply this procedure to an invasion by the snail *Batillaria attramentaria* in San Francisco Bay, California, to show how from
nearly zero starting information we can empirically test eradication feasibility and
design an actionable campaign.

4.1 Introduction

Invasive species are one of the leading environmental challenges of our day.
Invasive species cause economic damages, loss of ecosystem services, and are
the second greatest cause of biodiversity loss worldwide (Wilcove et al. 1998,
Mack et al. 2000). Under international regulation, and of their own volition, many
countries worldwide have mandates to take aggressive action against invading
species (Genovesi and Shine 2004). Effective management of invaders can re-
duce their harm but is often a matter of balancing aggressive responses with
practical considerations of feasibility.

The most aggressive response to an invasion is to eradicate the invader. A
successful eradication, especially an early one, can negate any deleterious
effects of the invader. However, since eradication failures are numerous and
attempts can be costly, there is justified apprehension in the ecological and
managerial community about eradication. Nevertheless, generalities have begun
to emerge about when eradication may be successful so as to avoid costly
failures (Myers et al. 2000, Rejmánek et al. 2003, Vander Zanden et al. 2010, Chapter 3).

To produce a general framework for evaluating the feasibility of eradication, the common characteristics of numerous eradication successes and failures have been used to identify the possible general pre-requisites for eradication.

Numerous authors (see Appendix B) suggest heuristics from terrestrial and marine examples. Pluess et al. (2012) take a data-mining approach and identify factors that contribute frequently to success in 173 worldwide eradication attempts. Bax et al. (2001) and Anderson (2005) review the legal, organizational and administrative requirements of eradication. Bomford and O'Brien (1995), Myers et al. (2000), and more recently Hoffmann (2011) also include ecological requirements generalized from case studies. Epanchin-Niell and Hastings (2010) and Chapter 3 highlight economics, examining the cost-benefit of eradication as a criterion. Many of these authors also discuss the required timing and scope of eradication and suggest protocols in order to achieve success.

These frameworks explore many dimensions of eradication and offer dozens of occasionally competing heuristics for eradication success, but none offers a complete picture of eradication planning. Some of these frameworks are too
vague, as in i) “eradication may not be feasible after the population has reached a certain size” (Genovesi 2001), or may not be completely general as in ii) all reproductive individuals must be vulnerable (Bomford and O'Brien 1995, but cf. Chapter 3). Some are too theoretical to be actionable, like iii) identify and then reduce risk (Bax et al. 2001), while others are too narrow and specific to one organism (Anderson 2005). These frameworks are valuable, and I do not intend to criticize these examples in particular. However, existing frameworks can veil the operational complexity of an eradication program. Despite effort to develop eradication frameworks over the past decades, many lack specific guidance on the quantitative experiments or measures and sequential steps that may be needed to evaluate eradication feasibility.

Existing frameworks aim to be omnibus tools to make critical, expensive decisions, and I identified 43 heuristics that they offer to guide eradication programs (Appendix B). It appears that some of these prescriptions are vague and will lack the quantitative guidance needed to operationalize an eradication program. In other cases, the recommendations are specific to particular taxa or habitats, and appear to lack generality. In addition, some elements do not appear to be strictly required for eradication. These assertions have not yet been tested though, as there has been little work to synthesize all these competing
frameworks and test their utility by applying them to novel invasions. Importantly, having many competing frameworks, rather than one synthetic framework likely hampers pragmatic response to invasions, so summarization and testing of these frameworks are overdue. Consolidating the best and most general features of all these frameworks into one concise framework will simplify the development of eradication programs and accelerate conservation efforts.

4.2 Eradication framework synthesis

To consolidate and evaluate the guidance of many available eradication frameworks, I summarized their key recommendations and applied them to a new invasion. The best way to test the generality of these frameworks is by applying them, in unison, in a system where they are all naïve. I used the recent invasion by the marine snail *Batillaria attramentaria* (henceforth *Batillaria*) as a model for this purpose. For each recommendation presented in the existing frameworks, based on my local knowledge of the invasion, I applied the recommendation to the infestation of *Batillaria* and considered whether the recommendation advanced a decision about the feasibility of eradication. I applied the recommendations to *Batillaria* as if I were a naïve to eradication. Following this exercise I could identify where recommendations were i) not general – where they recommend something that is not strictly required to
advance a decision about eradication, or did not seem to apply to the *Batillaria* case or ii) were not practically applicable (i.e., vague) – where the recommendation was not actionable or could not be framed as an experiment, or iii) were contradictory to a recommendation in another frameworks. In Appendix B I present the result of applying each recommendation to the *Batillaria* case. When a recommendation failed one of the three tests (generality, actionability, contradiction), rather than dismissing the recommendation, I attempt to reconcile the limitations when possible. Guidelines that are not always required may have specific conditions under which they are needed and so conditionals may be used to structure these guidelines into a decision tree. Guidelines that are too vague may be quantified so as to offer specific experimental guidance to evaluate eradication. Where the frameworks disagreed, I can excise their contradictory guidelines. After following this procedure I produce a synthetic framework that is organized as a decision tree, and contains fewer, more quantitative guidelines, all derived from existing frameworks. Rather than making one more eradication framework I sought to synthesize, simplify, and standardize existing frameworks.

Several frameworks recommend that the time, personnel, budget (e.g., Usher 1989, Rainbolt and Coblentz 1997, Vander Zanden et al. 2010) and probability of
success (e.g., Bomford and O'Brien 1995, Vander Zanden et al. 2010) of eradication should be estimated ahead of time, but few of the available frameworks outline strategies for transitioning from experiments to design of a program. I categorized the guidelines in Appendix B and where the existing frameworks offer operational parameters they tend to center on either the required timing or scale of treatment necessary to achieve eradication. Of the guidelines which offered operational guidance, 78% concern themselves with one of these important features (Figure 4.1).

These are not surprising findings; populations growth is dynamic and spatial and temporal variations in the vulnerability of species are widespread in nature from increased vulnerability of young organisms to the relative immunity of those in seasonal burrows. As such a simple time budget for eradication may not apply and careful timing of treatment is often required. Biological and spatio-temporal issues such as these can affect when, where, and how treatment may be conducted and these patterns may shift with time. Many frameworks make this observation and agree that timing and targeting treatments to exploit these oscillating vulnerabilities is a key to effective eradication (e.g., Myers et al. 2000, Courchamp et al. 2003, Brockerhoff et al. 2010).
Eradication will not always be feasible, of course, and each element of the decision tree also forms a specific test for eradication feasibility – thus the outcome of each step is either a dismissal of eradication or a constraint on the necessary timing or scope of treatment. Where an element in the tree suggests eradication failure, no further experimentation is required and if the entire tree can be traversed then eradication may be possible, based on the timing and scale parameters from all experiments. This approach is often referred to as a fault tree and has a history of application in invasion management (Hayes 2002).

Figure 4.2 shows a flowchart procedure constructed from the process above. In each section below I review the set of experiments that form the flowchart. The suggestions from the frameworks can be grouped in three experimental sections: treatment, delimitation, and immigration. Each of these categories offers groups of experiments to estimate timing of scope of eradication. My procedure is derived from existing frameworks, and a bracketed number is provided in the following sections to indicate the corresponding framework(s) that addressed the respective issue reflected in the procedure (e.g., [10] refers to row number 10 in Appendix B).

4.2.1 Treatment
Effective treatment is probably the most obvious requirement of eradication success [35]. The efficacy of a treatment is measured by what proportion of individuals it kills and at what rate. Bomford and O’Brien (1995) stated that the rate of removal must exceed the rate of increase [6] and that all reproductive individuals must be vulnerable [7]. Chapter 3 shows how eradication is possible without direct treatment of all age groups and present mathematical criteria for eradication given efficacy per age class and treatment rate, offering a generalized quantitative approach and explicit equations to calculate timing demands relative to treatment rates [33].

To estimate required timing to eradicate a species, Chapter 3 demonstrates the vulnerability time window (Figure 4.3). Many treatments will miss individuals based on age class (i.e., missing tiny juveniles) but as these individuals age they may later become vulnerable (Buhle et al. 2005). The vulnerability time window defines the period of time within which treatment must be repeated – to dispatch those missed individuals once they are vulnerable, but before they are mature. If a treatment is highly effective on older age classes (≥tv, the age of vulnerability; Figure 4.3) but misses younger individuals (<tv, Figure 4.3) then another treatment must be conducted before the missed individuals reach maturity (tm; Figure 4.3) or pass beyond the vulnerability time window, tw. The time \( tw=tv - tm \)
defines the vulnerability time window, within which another treatment pass must be conducted. In a system with $N$ interconnected populations each treatment pass must treat all $N$ populations and return to retreat the first before the missed juveniles mature and produce larvae (or seed) of their own (or mature past the vulnerable time window). By executing well-timed treatment passes in this way, no new adults are produced and if the passes are continued eradication will succeed. I use their quantifications throughout to allow me to define when eradication is likely infeasible.

The first experimental priority should be to identify treatments that are effective on at least some pre-reproductive age class. If a treatment is not uniformly effective on all age classes, repeated, well timed passes will be needed. Therefore, treatment experiments should record the efficacy of treatment across age classes as well as the rate of the treatment, and further experimentation may be required to determine the maturation rates of the target species in order to calculate the frequency of those passes (see Chapter 3 and Appendix A for a demonstration). Additionally a researcher should be careful to consider explicitly potential spatio-temporal variation in vulnerability to treatment. For example, in coastal marine systems, efficacy may vary by habitat type (such as rock, sand,
mud, or vegetation), and there may be times where the species is immune from
treatment (i.e., a refuge, like if the species is covered by high tides once per day).

As illustrated in Figure 4.2, failure points at the treatment stage include: i) when
no effective treatment is available, ii) the available treatment cannot dependably
kill at least some age class of pre-reproductive individual, or iii) if individuals may
remain and reproduce in refugia before first becoming vulnerable. If failure
occurs at any of these points then research into control (versus eradication)
strategies, or investment in alternative treatment options, are advisable.
Otherwise, delimitation research should proceed.

4.2.2 Delimitation

Delimitation is required to define where the eradication must take place and
determine the number of infested areas to be targeted [14]. Eradication may be
possible without delimitation, but uncertainty will be high – likely diminishing as
delimitation effort rises. Delimitation experiments, later combined with
immigration experiments determine the scope of an eradication effort.
Delimitation can also help identify spatial heterogeneity of effective treatment
rates and temporal variance in vulnerability which further constrains when and
where work can occur. All of these spatio-temporal differences in vulnerability
and treatment rate must be mapped. The failure point at this stage is if delimitation is not possible (Panetta and Lawes 2005, Leung et al. 2010). Delimitation experiments may also identify refugia not known during treatment phase; eradication is unlikely if individuals could remain in these refugia long enough to reproduce without first becoming vulnerable.

4.2.3 Immigration

Depending on the scale of movement and the life stage involved this movement can be referred to by many names in ecology (e.g., dispersal, re-invasion, recruitment, mobility). I group all these modes under the term immigration.

Some frameworks have suggested that eradication may not be possible once the population reaches a certain (non-specific) size [2]. More specifically, the maturation of new adults must be prevented within some set of treated areas via treatment passes. The challenge is to determine a manageable scale of these treated areas and this is done by examining population exchange after delimitation has located populations. Some frameworks note that immigration during eradication must be halted [4]. Rather, I argue that immigration can inform required timing and scope. Ideally, immigration should be prevented, but as a criterion, treatment must only be rapid enough to prevent new adults from
forming in treated areas and not have this work undone by immigration events, otherwise barriers must be erected to prevent immigration.

In the common situation that treated areas exchange pre-reproductive populations with one another then all populations must be treated before pre-reproductives missed in the first population mature past the vulnerable time window (i.e., all populations treated within the length of the time window). Unless barriers to this immigration are available a manager should scale down the treatment area to a scale at which this rate is achievable. The number of populations that can be treated in this time (of the size of a contiguous population) will define the local scale of the project. Each time a population is treated individuals of ages within the vulnerability time window are extirpated. As individuals younger than the time window mature and while treatments are ongoing on other populations these individuals enter the vulnerable window; repeated treatments are timed so that they will be retreated before they exceed the window or mature. Immigrating individuals of ages within the time window can interfere with this procedure.

If immigrating individuals are within the time window then treatment passes must be rescheduled. Effectively, this means narrowing the vulnerability time window
and recalculating the scale and timing of passes. As ever passes must be repeated before missed individuals reach maturity or pass the new window, but now these missed individuals include immigrants and those younger than the vulnerable window, so the frequency of repeated treatments must be accelerated. The local scale must be redefined to include the greatest number of populations that can be treated within the new window. If the immigrants are adults then barriers must be erected since the repeated passes are meant to prevent individuals from maturing in treated areas and immigrating adults will preclude this. If the local scale includes populations that a disparate enough so as not to exchange populations on the time scale of eradication then these populations can be considered independent. Populations that are isolated during eradication can be excluded from the time window criteria – rather than having to treat all of these populations within the time window a manager should just treat as many as possible.

Repeated treatments at this local scale will prevent new adults from forming, but immigration into this local zone from populations outside can interfere with eradication. If immigration is limited and only re-infests a portion of a treated area during treatment then tiled, overlapping treatments may be conducted. For instance, if a manager can clear a football field up to the goal line (18 yards) in
two weeks, but within two weeks the leading 8 yards are re-infested, then the eradication must resume at the 10 yard line the next time. If the extent of immigration into the treated area is total, meaning the entire newly treated area is subject to immigration (or unknown) then eradication may not be feasible.

Effective eradication is a matter of careful timing, and the data required to make judgments is specific and concise. Immigration, if not controlled by barriers, can force quicker timing or shrink the scope of eradication possible. The failure point is if this quicker timing cannot be achieved, even at some small scale. At the local scale, immigration need only be evaluated if treatment is incomplete and nearby untreated areas can infest untreated areas. Due to the global nature of invasions, and the connectivity of invaded areas, re-invasion (i.e., immigration from external sources outside the purview of eradication, outside the local scale defined above) may be inevitable, so meso-scale immigration (sometimes called re-invasion at this scale) must always be examined [42]. If eradication is not worth repeating on the time scale of re-invasion then treatment must be expanded. If, for example, dandelion seeds blew into the stadium from a nearby stadium about once every two years, the manager would have to re-clear the stadium about every two years or would have to treat all stadia within the region. These estimates can be difficult to make, as re-introduction events are not
deterministic processes and the shape of this function can be important, but regardless the failure point from re-introduction is a matter of cost-benefit.

4.2.3 Cost-benefit

There are many instances where eradication effort may not be worthwhile, especially when treatment is on a very small scale, or when many treatment passes must be repeated frequently. This cannot be determined until the costs of the eradication program are estimated. If neither treatment nor delimitation experiments trigger failure points then an eradication program must be drafted that satisfies all the timing demands of all experiments and its total cost must be weighed against the benefit of eradication. Eradication may be perfectly feasible but may still be unadvisable due to its cost relative to the benefits of conducting the eradication. Other frameworks have emphasized the importance of the general usefulness of eradication [3], and targeting species whose damages can be halted by eradication [20], but I follow those that recommend a more formal cost-benefit analysis [11].

4.3 Case study

To examine the utility of all the frameworks, I begin with a system about which very few data have been collected, which has not been used as a case study for
any eradication framework, and where an invader is established. I work from the bottom up using my procedure to design experiments to test eradication feasibility and the timing of treatment required. I apply this effort to a current invasion of an intertidal snail *Batillaria* in California. Eradication was explored previously in the system, but the program was advanced at a small (pilot) scale and generated haphazardly, rather than using more formal analysis of feasibility. As a result, the potential for eradication remained unclear, despite the time and effort spent. I will revisit this invasion and through structured experiments test the feasibility of eradication and determine the timing and scale of treatments necessary for success. Timing and scale demands may be translated easily into resource requirements so I will examine the total cost of a management program built to meet these demands. I remind managers that earnest eradication attempts require careful evaluation – and can be facilitated by the adoption of quantitative frameworks.

4.3.1 Study species and system

*Batillaria attramentaria* (Crosse 1862) (=*Batillaria cumungi*, =*Batillaris zonalis*, (Yamada 1982, Wonham et al. 2005), commonly known as the Japanese mud snail, is an invasive mollusc from Japan and Hong Kong (Byers 1999). It was introduced some time prior to 1935 to the Pacific coast of North America (Miura
et al. 2005). It overlaps its range with, and is a close ecological analogue to, the native California mud snail (\textit{Cerithidea californica}) (Byers 1999). Where the two co-exist, the invasive snail is able to out-compete the native species and has resulted in native displacement. Furthermore, \textit{Batillaria} is an ecosystem engineer and can facilitate subsequent invasions. It has been shown to provide hard (shell) substrate to the invasive Atlantic slipper shell (\textit{Crepidula convexa}), the Asian anemone (\textit{Diadumene lineata}), as well as some native species (Wonham et al. 2005). This species occurs elsewhere in California but was recently detected in the San Francisco Bay after an unauthorized movement of oysters from an adjacent bay, where \textit{Batillaria} is known to occur, suggesting a likely mechanism for introduction (C. Zabin, pers. comm.).

Within the San Francisco Bay, USA \textit{Batillaria} is thought to be limited to a single marina and the adjacent shore, but there is concern about spread to the wider San Francisco Bay – already one of the most invaded marine systems in the world (Cohen and Carlton 1998). \textit{Batillaria} is an intertidal species (Adachi and Wada 1999) and occurs on the intertidal in Loch Lomond Marina, to the east of the bay near San Rafael, California. This species occurs on muddy, sandy and rocky substrata. Although \textit{Batillaria} produces crawl-way young and forgoes larval dispersal, it is mobile (Lafferty and Kuris 2009) and has managed to occupy
much of the intertidal area of the marina since 2006. In 2006, a pilot project was initiated to test a method to eradicate *Batillaria* from a small area at Loch Lomond Marina (TBI 2006). A treatment was immediately obvious (hand picking) and over five days 120 volunteers removed over 69,000 snails from a small area, which was quickly recolonized from an adjacent area, and the invasion persists.

4.3.2 Experiments

Prior trials of treatment methods had identified flame treatment as a potential treatment so I limited my treatment experiments to this one method. I timed the treatments, and after treatment I examined samples under a microscope to count the number of snails alive in each size class (to test the efficacy of treatments on different age classes and examine demographic response to treatment). In a few areas with rocks I timed removal of rocks to expose shore to flame. I repeated these treatment experiments in many different substrata to examine spatial variability. I then mapped the different substrate types within the marina. Of course many other forms of treatment are available in different systems, but the consistently important piece of information is the efficacy across age classes, rate, and spatio-temporal homogeneity with which it removes individuals.
I examined the distribution of the snail within the marina and was careful to note any possible spatio-temporal refugia the snail could exploit to evade treatment. In Loch Lomond it was known that the snails occupied the entire horizontal extent of the marina, but their distribution on the vertical or elevation axis (from intertidal to subtidal) was unknown. Thus it was not clear how low into the inter-tidal my treatments would have to extend. In Loch Lomond I took sediment grabs at various levels of the intertidal to look for the presence of *Batillaria*. *Batillaria* move surprisingly fast (Chan and Chan 2005); snails removed from one area in Loch Lomond could be replaced by mobile reproductive adult snails from a nearby untreated zone on an hourly scale, so I was compelled to use barriers to block exchange between local untreated and treated populations. I also tested the efficacy of copper tape and Tangletrap (a commercial resin) at blocking the movement of snails.

4.3.3 Experimental results

Flame was indiscriminate in the age groups it killed and was able to heat the sediment sufficiently to kill snails at depth in hard or medium-hard sediment after 2 and 4 minutes, respectively, leaving no snails alive in any of my trials (Figure 4.4a,b). In cores taken from my treatments no snails were ever detected below a depth of 4cm, similar to depths found in Japan (Kamimura and Tsuchiya 2004).
In soft sediment flame treatment was unable to heat the sediment sufficiently to kill snails at depth after 4 minutes (Figure 4.4c). Later experiments found flame treatment up to 20 minutes was ineffective in this substrate. I speculate that this was due to water retention in the sediment and its dissipation of heat. As a fallback, manual removal was effective, but the method employed was different than the one used in the original eradication effort. This manual removal involved carefully removing mud from a quadrat to a depth of 4cm. The removed mud is then heated by flame on a brick surface for 5 minutes and returned. This method took longer, 8 minutes per square foot (0.09m²), but was completely effective.

The various substrate types require different treatments and mapping of these sediment types revealed that the Loch Lomond system is a patchwork of sediments types. Therefore the required time to treat a given area will be heterogeneous in Loch Lomond. Generally, substrate hardness increases moving away from the water, but exceptions abound. Sediment grabs along four transects in the marina found no snails below a tidal elevation of MLLW+1 ft (0.30 m; Figure 4.5).

Such tidal elevations would be exposed by low tides frequently, but irregularly throughout the year. This region of California has mixed semi-diurnal tides (i.e.,
two high-tide events and two low-tide events of differing magnitudes each 24 hours). These tidal patterns are predictable, but can result in shifting time and magnitude of low tides throughout the year resulting in dynamic days and times at which the tide falls below MLLW+1 ft (+0.30 m). Therefore, the lower intertidal is a spatio-temporal refuge from treatment, but careful timing of treatment can overcome this.

Flame treatment was ineffective in the presence of large rocks, and removal of rocks larger than fist-sized took 0.16 minutes per person per square foot (0.09m²). For example, since the tide rises and falls with time, snails in the lower intertidal are only available to treat at low tide, following a strict tidal schedule. Also, treatment methods in some substrates were slower than others and these varying rates had to be mapped to treatment could be tiled and coordinated.

In laboratory experiments I found that this species of snail would willingly cross a TangleTrap barrier, but were unwilling to cross a barrier of copper tape, even when tempted with food or repelled with bright light, and even after one month of copper oxidation (Figure 4.6). I designed a three-part barrier: lead line at the bottom to form a tight seal with the sediment, fine mesh body, and floating top
that rises and falls with the tide, topped with copper tape to keep snails from climbing over the barrier.

4.3.3 Designing an eradication program

Since all age ranges of *Batillaria* are uniformly vulnerable to treatment, treatment timing is not constrained by the need to return for multiple passes. However, since snails are not vulnerable when they are underwater, vulnerability varies spatio-temporally along the intertidal as the tide rises and falls with time. Furthermore, since the marina is a patchwork of sediment types that have differing treatment rates, timing of treatments must be carefully co-ordinated to ensure treatment of all the different patches (at their various treatment rates) within a target area before the tide covers the area for the day. A team of workers must be scheduled to work only on days with tides that fall below MLLW+1ft – the lower limit of the snails’ vertical limit. On each of those days the team must be able to treat all the various substrate types (at various rates) within their assigned area with a combination of torches and manual treatments before the tide returns to conceal it. The area assigned must be small enough so that it can be treated before the tide returns to cover it. Larger teams and sections with simpler substrate will allow for larger areas of treatment. At the end of the day the team must lay a barrier to isolate their treated area (but this could be done by
boat at high tide). On the next day with appropriate tides, the team must treat the adjacent area (for simplicity, and to minimize barrier use). These spatio-temporal variations in vulnerability require careful timing and greatly constrain an eradication program.

Immigration can occur from two sources: inside, and outside of the marina. Exchange among local populations inside the marina undergoing treatment can be controlled by barriers and these must be deployed by the treatment team after each zone is treated. There are also two populations on either side of the marina that I do not consider treating. The two populations outside of the marina are separated by two small land barriers on either side, totaling < 1 km length and between 10 and 50m width. The populations pose long-term re-invasion risk. The snails may be unwilling to cross it themselves but they could be carried across inadvertently by humans. The rate of immigration at the larger scale is a rare event and its rate is unknown and hard to measure. I suggest that a barrier also be employed at the larger scale to restrict human movement over these two small land barriers. While this rate is (and often will be) unknown, I presume that re-invasion will occur on the scale of years, but I examine the implications of a range of values for the effect on eradication feasibility.
I built a computer model to simulate the complex scheduling of an eradication program that could be executed within the timing constraints above (details are in Appendix C). The model results indicate that eradication is onerous, but possible. The total time to conduct the eradication ranged two orders of magnitude from 10-1000 days (Figure 4.7). Teams of 1, 2, 4 or 8 people would be unable to complete the eradication within 10 years (the upper limit of my consideration). More people on a team generally accelerated the eradication but suboptimal start day could override the time savings of having a larger team. For example, starting around March 11, 2014 (the 800th day in Figure 4.7) a team of 57 people would take as long as a team of 215 people starting around Dec 1, 2013 (the 700th day in Figure 4.7). Due to the tides there are tracts of days on which no treatment is possible. An eradication program that started before one of these periods, or that spanned many of these tracts, would take longer overall.

The total effort to treat the marina is a fixed value of about 14,500 person-hours, imposed by the sediment types and their various rates of treatment, and is independent of team size or start day. In addition, the total effort of a program includes the per day effort of setting up a barrier and the per-day, per-person effort of travel. These add 1000-2000 person-hours but are small compared to the total effort required to treat the entire marina and their contribution is hardly
noticeable. There are local minima in total effort that depend on start day which are periodic with the tides.

4.4 Cost-benefit

While the model indicates that a carefully coordinated effort with tens or hundreds of workers could eradicate this species, and while it is tempting and perhaps justified by the precautionary principle to eradicate this invader (Kriebel et al. 2001), I must also consider monetary factors. Research on the full range of impacts of this species are limited, and its effects within the marina are unknown, but likely limited. For this reason, it may not be worthwhile to eradicate from a cost-benefit perspective. *Batillaria* presents no known future economic risk in the marina, either. The primary species they threaten, *C. californica*, is not commercially viable and is not found in Loch Lomond marina, and thus any benefit of the removal of the snails would have to be measured in non-market way (e.g., the value of a pristine marina). The cost of the *Y* year eradication program, expressed in today's dollars, $C$, is,

$$C = \sum_{i=0}^{Y} \frac{W_i \cdot 14500}{(1 + D)^i} + C_F$$

Where $W_i$ is the hourly wage paid in year $i$. If I take the wage to be California’s minimum wage of $8 (USD hereafter) and assume a rise of $0.5 per 3 years, and assume a discount rate, $D$, of 5% then in the 10 year eradication
scenario the total labour cost is $108,000 in today’s dollars. The marina should be able to operate normally during the eradication. The material costs \( C_F \) would add about $257,000 dollars to the total costs based on $15 per person-day torch rental and $200 per day boat rental and $2500 per year barrier costs. This assessment could change if, for example, the snails spread within the wider San Francisco Bay and the scope of their impact expands to realize some hitherto unknown impact. An eradication program that would cost in excess of $350,000 to remove a species with no known economic damage may not be considered a priority. Also, I did not consider treating the adjacent populations so the true cost would be many multiples of this cost to either expand the treatment area to include those areas of to retreat the marina periodically upon re-invasion.

4.5 Additional recommendations

With respect to the management of *Batillaria* in Loch Lomond, I need not consider any more of the guidelines from the frameworks. However, for completeness I summarize the guidelines to consider when launching an eradication program. Efforts should be made to recover the system after eradication [17], but only when this is a stated goal of eradication, as these goals should be outlined in advance [37]. Access to private land (as needed) should be secured in advance [13]. This should include permitting as some jurisdictions do
not differentiate invasive species removal from other environmental impacts. The role of each participating agency should be clearly defined [27] and public consultation should examine the socio-economic concerns of the invader [29].

Consultation should take place at a local level and involve stakeholders (i.e., those affected by eradication) [41]. This should include public consultation since negative public perception of eradication has halted other projects (Genovesi and Bertilino 2001). Anderson (2005) felt that this local-scale involvement was critical and that most successful eradications would be bottom-up programs guided by motivated, locally-knowledgeable managers [43]. Shine et al. (2010) highlights that high-level governmental involvement also may be required to ensure appropriate legal status of the invader [28], cross-boundary consultation [30] and development of national-scale actions [31]. A treatment program must be followed by monitoring to access success of the project and to detect new incursions [32].

4.6 Discussion

In order to advance the development of general, actionable eradication frameworks we must move from theory to application. I show how no single framework offers enough guidance to design the eradication of an arbitrary invader, but how they can be combined and modified to better do so. I
summarize 43 different eradication heuristics from dozens of papers and divide them into categories. Several offer (or can be modified so as to offer) useful experiments to establish quantitative constraints for eradication. I organize these experiments to form a concise procedure that is more general than any of the parent frameworks. I show how this procedure can be applied to evaluate the feasibility of eradication and, if feasible, to estimate the timing, duration, scope, and cost of a final eradication program. I review other guidelines that offer further recommendations like administrative and legal best practices that are useful to examine before launching an eradication program. It appears that several other heuristics are not of general use but specific to particular circumstances. These, I caution, can unnecessarily prolong the research phase of an eradication program and lead to magnified impacts.

Never have all these frameworks been applied in combination to address a novel eradication challenge. In addition to distilling and organizing the most practical guidelines offered, by applying these guidelines to a system about which they were naïve, I was able to reveal a few short-comings and, by modifying them, add some additional generalities they had not considered. I replace vague prescriptions and excise unnecessary ones. For example, eradication may not require all individuals to be vulnerable [7], instead only pre-reproductive
individuals must be vulnerable. Rather than dismissing eradication in the face of imperfect treatment, I recommend experiments to determine the efficacy and rate of treatments. Rather than opaquely suggesting intervention based on basic biology of target species [15] I recommend determining the vulnerability time window from maturation and treatment rates and using that to calculate the number and frequency of treatment passes. I agree that delimitation is important [14] but add that it can be used to determine necessary treatment rates – a manager must treat the entire infested area within the time window (or conduct overlapping treatments therein). Immigration need not be reduced to zero [as suggested by 4], but retreatment of untreated individuals must be timed so as to overlap immigration and this fact can be used to determine the timing and scope of treatment. Instead of vague prescriptions like maintaining continuity of treatment [8], I suggest sets of experiments to determine the precise timing required for eradication, and show how these experiments can define bounds within which eradication programs must be fit. Eradication is then a matter of adding resources to meet these timing demands (if this is economically suitable). My procedure aggregates and improves the best advice from all the frameworks and presents it in an easily navigable decision tree to optimize rapid response.
There were several additional experiments recommended by the frameworks that are not generally required, and which I did not conduct. A minimum viable population [23] is hard to measure in situ and I feel that its quantification would retard action. Furthermore it is not required if effective treatment is available and should probably not be depended upon for eradication success if effective treatment is not available. Allee effects can allow eradication even with ineffective treatments (Liebhold and Bascompte 2003) [21]. No existing eradication frameworks offer quantitative advice on the probability of eradication when treatment methods are haphazardly effective. My framework summarizes and organizes existing frameworks and thus offers no recommendation when treatments are unreliably effective. I do not dismiss Allee effects, but I ignore them in my analysis due to their notorious difficulty to study (Courchamp et al. 1999), and the uncertainty and risk of an eradication predicated on Allee effects. The lag period between establishment and subsequent spread [24] is only required if re-introduction is likely. Genovesi (2001) recommends priority of treatment is given to immigrating propagules [18]. The rare events that lead to immigration in Loch Lomond can be given priority treatment, but only if contingency plans are in place to rapidly detect and respond to incursions [38]. It has been generally prescribed to concentrate effort during time of greatest vulnerability [16], but I have quantified this much more precisely – however, I do
encourage managers to exploit any seasonal vulnerability that their target species may have, in addition to the timing I provide.

I concentrated my synthesis on the most practical elements of eradication design and decision making. The frameworks recommend a number of other treatment considerations, which warrant consideration while conducting treatment experiments. Genovesi (2001) and Morrison et al. (2007) warn that treatment can alter its own efficacy by shifting demographics (i.e., dispersal, fecundity) or altering behavior (i.e., avoidance of treatment) [9], so treatment experiments should monitor for such effects. Although I did not formally test for these effects, there were no conspicuous changes in behavior or dispersal observed during my tests.

This, as with most eradication programs, requires highly effective methods and requires that the methods remain highly effective after being repeated many times by different people. Flame treatments may be less susceptible to human error, especially if they can be mechanized to a greater degree. Manual treatments, in the areas that require them will demand meticulous, careful work and a dedicated team. Although my analysis included a team of 414, it is probable that such a large team would be difficult to manage and that they would
perform slower than predicted or fail altogether. My eradication program is based on known, simplistic treatment techniques and could change if better tools are developed. One sensible recommendation for a manager determined to eradicate may be to develop more efficient, scaled-up treatments to an industrial sized instruments like some large earthmover or larger heating tool as this would both accelerate treatment and reduce human error. Updated methods could easily be re-examined by my framework.

The limitations of my summary procedure are the same as the limitations of existing frameworks, but these represent the state of the art of eradication frameworks. I outline some of the limitations here, but eradication can be an esoteric process and I do not believe that my procedure is a universal tool to eradicate invasive species. I do, however, strongly encourage environmental managers and ecologist to incorporate their own eradication experiences into this framework. The feasibility of the experiments proposed herein is not fully known in other systems, but many are based on basic biological research that has been ongoing for decades: the distribution, maturation rates, dispersal potential of organisms. Future work could examine where this type of experiment would be infeasible and perhaps develop alternatives. As I have taken the experience of other authors and modified, re-organized and improved upon their work I hope
others will do the same of this framework and that we can build toward a
universal framework for eradication.

Upon revisiting the case with more quantitative tools and rigorous analysis, I
consider the eradication of *Batillaria* in Loch Lomond marina feasible but perhaps
too costly. No pre-requisites of eradication seem violated – none of the failure
points were triggered in my experiments. I considered *Batillaria* as a thought
experiment for eradication. In searching for a system to apply my ideas I did not
look for the most menacing invader, I wanted a small system with high levels of
local support and many treatment options. *Batillaria* in Loch Lomond met these
requirements, and allowed me to develop an eradication pilot program to develop
and test my procedure. Although future work could examine the required
treatment of the two adjacent populations, after studying just the marina I was
able to estimate the total effort required for a local eradication of the highest
priority area and on that basis alone I was able to rule eradication challenging.

Had I examined the two adjacent populations and the transmission between
them, it is clear that my result would not change and eradication would remain
unwieldy. This demonstrates how my framework can be used to study only what
is strictly needed to make a judgment about eradication. I have shown how my
procedure can be applied in a real scenario by designing a complete eradication framework for \textit{Batillaria} from a start point of almost zero data.

My cost-benefit analysis of \textit{Batillaria} presumes the invasion does not spread. If \textit{Batillaria} threatened some damages in the wider San Francisco Bay my calculus may change, and those damages may be high enough to motivate a strong response. An eradication effort should consider non-target impacts as well [5]. A common, if somewhat crude, analysis of these impacts is to estimate the cost of these non-target damages and add them to the cost of the eradication. This type of analysis would fit easily into my framework when estimating costs but here I have not explicitly considered the possible costs of non-target impacts. However, the marina is an artificial system containing primarily non-native species, there are no known endangered species within the marina, and it is very likely that native species could recolonize the marina after eradication. In fact, re-colonization of native species after eradication may be generally advisable as a restoration goal.

I provide the most complete procedure to date to test eradication and to design an eradication program. My work is built upon established eradication frameworks from academic and governmental literature. I hope that future efforts
can employ my procedure to make informed, quantitative decisions about eradication and recover and restore many ecosystems from the damages of invasive species.

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References


Lafferty, K. D. and A. M. Kuris. 2009. Parasites reduce food web robustness because they are sensitive to secondary extinction as illustrated by an invasive estuarine snail. Philosophical Transactions of the Royal Society B: Biological Sciences 364:1659-1663.


Figure 4.1: The number of guidelines grouped into each of four categories. The bar for operational guidelines also shows the number of operation subcategories: other, scope, and timing.
Figure 4.2: The decision tree of my framework. Each box represents an experiment or measurement and the arrows guide the reader through the outcomes of each. Diamond shapes represent terminal outcomes of eradication testing, and the oval indicates where to begin. The bullet-shaped element labeled ‘AND’ indicates an “and gate” meaning to proceed if both depended boxes are
satisfied. \( t \) is the rate of treatment; \( tm \) is the maturation age; \( tv \) is the vulnerability age; \( N \) is the number of populations; \( R \) is the re-invasion rate; \( C \) is the cost (of eradication); \( B \) is the benefit (of eradication).
Figure 4.3: The life cycle eradication diagram from Chapter 3. The circumferential axis indicates age and the radial axis indicates the relative abundance of the age class. Marks on the circumference denote transitions from one age class to another (larval, juvenile, and adult). The wedge in pink marks the vulnerability.
time window, beginning at age $tv$ and ending (in this case) at $tm$, the age of maturity.
Figure 4.4: The number of *Batillaria attramentaria* left alive after treatments of varying lengths by flame. The x-axis is common among all three plots and indicates the experimental length. Plot a) is medium substrate, b) is soft substrate, and c) is hard substrate.
Figure 4.5: A plot of the number of snails found at each depth in the subtidal. The x-axis shows the depth calibrated to MLLW (in ft; 1 m ≈ 3.28 ft). This plot pools the results of 3 subtidal surveys conducted in Loch Lomond Marina.
Figure 4.6: A picture of a copper tape trial after one month of copper oxidation indicating the refusal of the *Batillaria attramentaria* to cross the copper.
Figure 4.7: A plot of the required number of days for eradication for various start days. The start day is the number of days since January 1, 2012. The different line styles indicate the results for teams of various sizes.
Linking statement 5

My final chapter builds upon the developments in the third chapter. The chapter adds explicit delimitation research at multiple scales, migration, spatio-temporal variation in vulnerability to generate a more complete framework for eradication. This chapter also adds the advice of 43 guidelines from numerous other published eradication frameworks by other authors. It distills and refines the advice from those frameworks (including Chapter 3) organizing them into a decision tree to evaluate the feasibility, scope, timing, cost, and research demands for eradication. The final chapter advances the science of eradication frameworks and presents the most complete, most general framework in existence. This framework, together with the advances this thesis has made to detection and eradication of invaders, advances our capacity to detect, remove, and thus limit the impacts of invasive species.
General conclusion

Invasive species are one of the leading environmental concerns of our day and their impacts are felt worldwide (Strong et al. 2008, Vilà et al. 2009). As the threat of invasive species grows we must develop new techniques to combat them more efficiently. A typical (or rather, an ideal) program will involve some form of defense to prevent incursions, a monitoring program to quickly detect incursion that were not successfully prevented and a control program to extirpate new invasions. My thesis offer new tools for the latter two critical elements of this program: detection and control.

One of the most frequently cited predictors of mitigating invasive species harm is early detection (Myers et al. 2000, Simberloff 2003, Pluess et al. 2012) but detection of marine invaders is still typically conducted in a haphazard manner (Fox et al. 2009). At the heart of this challenge is forecasting the future locations of invaders. I show how a common form of model (a species distribution model, or SDM) – with a long history of species distribution forecasting – can be adapted to capture key biological traits of a target species, and how this adapted model can forecast the patterns of the species. I show how these model forecasts can be specifically used to design monitoring programs and I apply my model to a harmful invasive species on the east coast of Canada.
I make substantive improvements to the state of the art in SDM. SDM have historically only included environmental predictors of species patterns, hinging entirely on niche theory. First, I explicitly include dispersal into my SDM. I confirm how dispersal is an important mechanism structuring patterns of species and vindicate many authors who have decried their absence from SDM. I show how these advanced SDM can be used to improve monitoring programs for a marine invader. Chapter 1 applies this improved model to *Ciona intestinalis* and captures estimates of several key biological traits like fecundity, temperature preference and dispersal. I then use the same model to design a monitoring program for another system at risk of, but not yet infested by, *Ciona*.

I demonstrate the importance of dispersal, in addition to environmental preferences, in forecasting larval locations. I model dispersal using a simple kernel function that estimates the proportion of larvae at given distances from adult sources. However, there are more complex, alternative models of dispersal like hydrodynamic models. Hydrodynamic models produce outputs of the final location of a larva (and its path), but do not typically model the environment-specific probability of recruitment that structure the true patterns of recruitment. Thus, the larval locations these models output are incompatible and not always comparable to the larval recruitment data typically collected in biological surveys.
and ostensibly used to validate these models. In Chapter 2 I produce a framework to compare among such incompatible models and demonstrate how such a framework can be used to examine the value of a hydrodynamic model of dispersal versus a simple statistical one, and how the advanced SDMs presented in Chapter 1 may be useful alternative models against which hydrodynamic models can be compared.

The first section of my thesis demonstrates the use of dispersal to improve models to forecast species locations. These methods are valuable contributions to dispersal model validation and SDM literature in addition to having demonstrable application for invasive species management. Prevention of invasions is ideal (Leung et al. 2006) but incursions are inevitable (Wotton and Hewitt 2004). A manager would be remiss if he did not consider what action should follow a positive detection of a target invader. This has motivated the development of rapid response tools that attempt to structure the response to new incursions. Tools like those developed in the first section can determine when such an incursion and are thus closely linked to any rapid response program (Wotton and Hewitt 2004). Despite the demand for rapid response programmes they are limited by the availability of scientific literature on control.
The results from my first section can be used to inform a rapid response protocol. The fit dispersal kernel from Chapter 1 could be used to guide rapid response – expected adult locations would be distributed around recruitment site according to the shape of the dispersal kernel. Chapter 1 does assume adult locations are known, however, but kernel results could still inform adult searches, and perhaps help identify other, previously unknown sources. Future work could refine these results and build a back-calculation framework that could adapt the framework from Chapter 1 to identify likely locations of adults based on a recruitment survey and would more directly inform a rapid response program. Likelihood methods developed in Chapter 1 could be adapted to estimate the adult locations (and kernel) that were most likely to have created the observed pattern.

Most authors favor eradication, when possible, in their rapid response programs (Locke and Hanson 2009). However, there are few frameworks available in the scientific literature to determine when eradication is possible or to guide its execution. This lack of eradication guidance has hampered action and has likely lead to eradication failures or a reluctance to attempt eradication even though it may be the ideal response. Chapter 3 introduces the first quantitative eradication framework which guides managers to exploit the life cycle of a species. The framework specifies the biological data required to estimate the number and
frequency of treatment passes to achieve eradication. In Chapter 3 I demonstrate how this framework can be used to guide eradication for the previously intractable eradication of *Ciona intestinalis* in PEI.

My final chapter builds upon the developments in the third chapter. This chapter adds explicit delimitation research at multiple scales, migration, spatio-temporal variation in vulnerability to generate a more complete framework for eradication. This chapter also adds the advice of 43 guidelines from numerous other published eradication frameworks by other authors. It distills and refines the advice from those frameworks (including Chapter 3) organizing them into a decision tree to evaluate the feasibility, scope, timing, cost, and research demands for eradication. Chapters 3 and 4 represent the most general, quantitative eradication framework to date. They are built upon biological fundamentals like life cycle, dispersal limitation and incorporate eradication guidance from dozens of other authors worldwide. The experiments they recommend are general and examine population features like spatio-temporal distribution, vulnerability to treatment, and maturation rates. These are common elements to nearly all invasions and should be generally feasible to collect in most systems.
Future work could include validation of a proposed monitoring plan as well as recruitment surveys in systems with a wider range of environmental conditions. Environmental data in the first section is for a single time and could be extended with a temporal model or further data collection to extend the forecasting of monitoring programs for other time periods. Further tests of SDM, dispersal-aware SDM versus hydrodynamic models are possible, including comparisons at larger scales and with settlement data instead of recruitment data. Future hydrodynamic models could be extended with more advanced biological behavior and validation with current data from deploys buoys. The second section of my thesis could be improved by incorporating monitoring more explicitly, as a subcomponent of my existing framework. Other sub-models could include one to assess the feasibility of eradication under imperfect treatment (i.e., attrition). Eradication may impose a selection bias when treatment is imperfect, and this should be included in an attrition sub-model. All this could be incorporated into an explicit population viability model to test thresholds for eradication. The existing framework could be tested on (and perhaps expanded as a result) on more species. The eradication frameworks in Chapter 3 presents the probability of success required to launch an eradication program but does not explore how to determine this parameter. Traditional approaches to this type of risk modeling involve estimating and multiplying relevant probabilities (sensu Johnson et al.)
2001). Future work could estimate these so that this eradication success probability parameter could be better estimated and incorporated into my framework.

In summation this thesis advances our capacity to detect and eradicate invasive species. Detection and eradication are crucial components of the invasive species management toolbox and the development herein of improved techniques for each could accelerate the management of invasive species and help conserve worldwide biodiversity.
References


When are eradication campaigns successful? A test of common 
assumptions. Biological Invasions 14:1365-1378.

Simberloff, D. 2003. How much information on population biology is needed to 

Strong, E., O. Gargominy, W. Ponder, and P. Bouchet. 2008. Global diversity of 
gastropods (Gastropoda, Mollusca) in freshwater. Hydrobiologia 595:149-
166.

Vilà, M., C. Basnou, P. Pyšek, M. Josefsson, P. Genovesi, S. Gollasch, W. 
do we understand the impacts of alien species on ecosystem services? A 
pan-European, cross-taxa assessment. Frontiers in Ecology and the 
Environment 8:135-144.

management: Developing incursion response systems for New Zealand. 
New Zealand Journal of Marine and Freshwater Research 38:553-559.
Appendix A

A.1 Costs

Below, I attempt to make order of magnitude estimates of the costs involved in my eradication strategy from Chapter 3. I have separated the costs by type of structure. The numbers presented are based on my own estimates and those made by academics and government scientists in PEI.

A.2 Docks

For estimates, I took every dock to have 3 supporting poles, 35cm in diameter every 3 meters (Jim Morriscey, pers. comm.). Another, solid form of dock, commonly called a Berlin Wall dock would have comparable surface area as the pole supported dock. The largest of the docks, located in Montague, with an estimated 150 poles (Garth Arsenault, pers. comm.) was taken as the upper bound for size of main docks – using this as an analogue for each bay’s main dock is an overestimate. Each bay has only a few smaller docks, each taken to be 30m in length. Additionally, again taking the Montague River as the model, each bay has 10 small, personal structures 10m in length. This makes for a total of an area on the order of 3000m² per bay. For five infested bays, the total is 15000m². The clearance rate was estimated at 4m²/hr. This yields 750 hours per bay. At 4 hours per diver-shift, this would be 187 diver-shifts per bay to clear all
public and private docks. A team of 10 divers could thus clear all docks and
wharfs in a bay in the twenty day time window. At an estimated $600 per diver
shift the total cost for all 5 infested bays would be $561,000 per pass.

A voluntary removal order for all temporary structures such as mooring buoys,
floating wharfs, and swimming docks would both decrease the cost and increase
the effectiveness of the effort. Most of the smaller docks could be removed from
the water with the co-operation of their owners.

A.3 Lines & Socks

Based on information from mussel harvesting operators, the costs of boat fuel
and labor per long line were estimated at be $100 and $150, respectively (Jeff
Davidson, pers. comm.). Based on 200 socks per line (Jeff Davidson, pers.
comm.), $0.40 per liter of vinegar, and 1L per sock of spraying, each line would
require approximately $80 worth of vinegar. This brings the total for spraying to
$330 per long line. I estimated this to be much less expensive than dipping and
equally effective (Carver et al. 2003). There are a total of 11110 mussel lines, as
estimated from the DFO economic analysis. 31% of these lines are in infested
areas (DFO 2006), so the total cost to treat all infested lines would be $1.1
million for each of the two passes required. The supporting lines and buoys
themselves could be treated in concert with the socks since they too must be lifted with the socks. This would be expected to add little to the cost or time required.

**A.4 Natural Structures**

From GIS data, the total area of infested bays (minus the newly infested Murray Harbour) is 67 km\(^2\) (Cambell 1973, MacWilliams and Judson 1973, Murchison 1973). The described area contains several different substrata. *Ciona* potentially settle on rocky substrata (2.53 km\(^2\)), but are likely sparse to absent in PEI (Locke et al. 2007). Given the sparseness, scouring would be limited mainly by swim and search speed because they would require little handling time to clear. I estimated a diver swim speed of 0.125 km/hr. to search every centimeter of the rocky substrate. Based on a 12-m swath of viewing, I estimated 5060 diver shifts, for a total of $3 million per pass. This effort would need to be conducted within the same time window as other structures, and would require as many passes as a dock. Based on these numbers, a team of 126 divers could achieve this in a 20-day time window. Given the ranges of this estimate, search rate should be validated before an eradication effort is started. While this would undoubtedly be a major effort, it is not unreasonable, given the potential gains.
I estimate the complete eradication to cost six $4.4 million; or if rocky natural substrates are not infested, $16.4 million.

A.5 Cost Benefit Calculations

By conducting a cost-benefit comparison I can estimate the potential gains of an eradication effort or estimate the probability of success my strategy must promise, or how long the invaders must be kept away for, for the management to remain financially reasonable. A case study that incorporates additional fuel, disposal, labour, and processing fees due to tunicates estimates a current $0.242 additional cost per kilogram of mussels due to tunicates (McDonald 2003). Based on production weight in the infested bays of 5575 metric tonnes, annual spending controlling Ciona in the infested bays totals approximately $1.4 million. Therefore, the estimated cost of continued treatment is:

\[
\begin{align*}
  c &= \sum_{i=0}^{\infty} \frac{1,400,000}{(1 + 0.05)^i} \\
  &\approx 28,000,000
\end{align*}
\]  

where \( i \) is the number of years the treatment is applied, and \( c \) is the total cost, using a 5% discount rate, as is typically done in economic analyses. Discounting can be applied to estimate present day value of future money. Thus, the benefit to cost ratio is $28,000,000 to $4,400,000, or a 4.76.6:1 ratio. Even with a %20 safety margin, this ratio would be 3.9:1. By my estimate, the eradication effort will cost $4.4 million, therefore, put another way, eradication would also be optimal if
there was a ≥16% chance of eradication or if it could keep *Ciona* to a level at which they had no impact on industry for 4 years.

\[
c = \sum_{i=0}^{4} \frac{1,400,000}{(1+0.05)^i} > 4,400,000
\]

A.2
References


DFO. 2006. An Economic Analysis of the Mussel Industry in Prince Edward Island. Department of Fisheries and Oceans Moncton, NB.


McDonald, C. 2003. What is the tunicate situation in Atlantic Canada? in Proceedings of the Atlantic Canadian Tunicate Workshop. DFO, Charlottetown, PEI.

## Appendix B

<table>
<thead>
<tr>
<th>Recommendation (from references in next column)</th>
<th>Reference</th>
<th>Application to <em>Batillaria</em></th>
<th>Category</th>
</tr>
</thead>
<tbody>
<tr>
<td>1 Early detection - Several frameworks highlight the importance of early detection. All else considered equal it does improve chances.</td>
<td>(Usher 1989, Myers et al. 2000, Simberloff 2003, Anderson 2005, Vander Zanden et al. 2010, Pluess et al. 2012)</td>
<td><em>Batillaria</em> were originally detected quite early, before they even spread to fill the marina. The eradication still failed.</td>
<td>Decisive</td>
</tr>
<tr>
<td>2 <em>Population size</em> - Eradication may become infeasible after the population reaches a certain size. The size is non-specific.</td>
<td>(Genovesi 2001)</td>
<td>I suggest that this element of eradication is entangled with available effort, and treatment rates. A large population that can be treated quickly is still eradicable. If the population cannot be delimited then no eradication – large</td>
<td>Decisive</td>
</tr>
<tr>
<td>3 <em>Usefulness of eradication</em> - eradication must be useful. For instance, an eradication program is not advisable if damages of the invader are irreparable.</td>
<td>(Genovesi 2001, Shine et al. 2010)</td>
<td>No measurable damages have been identified by <em>Batillaria</em>. Arguably, an eradication program with no detectable impacts should not be a priority. This relates to cost-benefit and is largely subsumed therein.</td>
<td>Decisive</td>
</tr>
</tbody>
</table>
| 4 | Immigration rate must be zero  
- Re-introduction must be prevented | (Bomford and O'Brien 1995, Myers et al. 2000, Genovesi 2001, Shine et al. 2010) | I show how this can inform timing and scope and how immigration can be overcome. I do dispute the generality of this criterion. A rudimentary cost-benefit can show that eradication may still be worthwhile if the eradication removes the cost of the invader for as long as it takes to recoup those costs. A million-dollar eradication can be repeated every year as long as it continuously, and assuredly prevents one-million dollars in damages. | Operational (timing) |
| 5 | Eradication does not cause (or minimizes) undesirable effects  
- often also called non-target impacts, the eradication harms species other than the one targeted | (Usher 1989, Bax et al. 2001, Genovesi 2001, Anderson 2005, Brockerhoff et al. 2010, Vander Zanden et al. 2010) | I have not explicitly considered the possible costs of non-target impacts. However, the marina is an artificial system containing primarily non-native species, there are no known endangered species within the marina, and it is very likely that native species could recolonize the marina after eradication. | Decisive |
<table>
<thead>
<tr>
<th>6</th>
<th>Rate of removal exceeds the rate of increase at all population densities - Two elements to this: i) rate of removal must exceed rate of population increase; ii) this must be true at all population densities.</th>
<th>(Bomford and O'Brien 1995, Genovesi 2001)</th>
<th>Edwards and Leung (2009) are more explicit about this. Rate of removal is only important for pre-reproductive individuals. Eradication can be achieved without any removal of adults.</th>
<th>Operational (timing)</th>
</tr>
</thead>
<tbody>
<tr>
<td>7</td>
<td>[All] reproductive individuals must be vulnerable (and detectable, even at low densities)</td>
<td>(Bomford and O'Brien 1995, Myers et al. 2000, Brockerhoff et al. 2010)</td>
<td>An eradication program can proceed without ever killing a single adult. If their maturation rates are known and if regular treatments can be maintained then eradication can proceed. As an example consider a hypothetical invasive bird. A small bird may be hard to remove but it must lay eggs in conspicuous nests at predictable times of the year. If treatment can be concentrated on those nests such that no new eggs are allowed to mature to adulthood then eradication can be completed within the lifetime of the extant adult bird population without ever killing a single adult bird. The imperative should instead read: (at a minimum) all individuals of a certain age range prior to extinction must be vulnerable.</td>
<td>Operational (timing)</td>
</tr>
<tr>
<td>8</td>
<td>Continuity of removal activities – specifically, a concentration of effort versus a protracted effort at lower intensity</td>
<td>(Genovesi 2001)</td>
<td>I agree that there is no need to take longer than necessary. My framework helps specify the timing required. Continuity is good in generally, but some timing constraints will mean there will be (acceptable) breaks in eradication (as was the case for the tide when treating <em>Batillaria</em>).</td>
<td>Operational (timing)</td>
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<tr>
<td>9</td>
<td>Caution about the effect of treatment on demographics - treatment may lead to increased fecundity, change in dispersal, or increase of immigration or emigration rates.</td>
<td>(Genovesi 2001, Morrison et al. 2007)</td>
<td>Changes in many demographics are inconsequential so long as treatment is maintained. My framework expects the production of new larvae, and this can be overcome with timed treatment so long as treatment is effective in high as well as low densities. Although I did not formally test for these effects, there were no conspicuous changes in behavior or dispersal observed during my tests.</td>
<td>Caveat</td>
</tr>
<tr>
<td>10</td>
<td>Time, personnel and budget must be carefully estimated and resources raised [ahead</td>
<td>(Usher 1989, Rainbolt and Coblentz 1997,</td>
<td>I agree. The challenge, of course, is how to devise the time, personnel, and budgetary requirements <em>a priori</em>. This is the heart of</td>
<td>Operational (timing)</td>
</tr>
</tbody>
</table>
any sensible eradication plan and the motivation behind the development of this framework.

### Cost benefit

The benefit of carrying out eradication should exceed its costs. The benefit could include non-market costs like the inherent value of nature (ref), but these are rarely considered due to their difficulty to measure.


I agree with the recommendation for this classic analysis. This is likely what will ultimately prevent the eradication of *Batillaria* in California.

### Probability of success

Probability of success of eradication should be evaluated [prior to eradication effort]


It is not obvious how to assign a probability to this important value. Instead, here I suggest that experiments can provide evidence in support of an alternative hypothesis of non-eradicable. If no experiment precludes eradication it is presumed to be possible.
<p>| | | | |</p>
<table>
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</tr>
</thead>
<tbody>
<tr>
<td><strong>13</strong></td>
<td>Access to private land (as needed) should be secured [prior to eradication]</td>
<td>(Bomford and O'Brien 1995, Anderson 2005)</td>
<td>The marina sits on private property but the marina staff has been very supportive of my efforts.</td>
</tr>
<tr>
<td><strong>14</strong></td>
<td>Delimitation of range – the extent of the invasion in space. This will define the area in which eradication must take place.</td>
<td>(Edwards and Leung 2009, Brockerhoff et al. 2010, Leung et al. 2010)</td>
<td>This was important both on the horizontal and on the intertidal (vertical) axis in California and is a core general requirement of my framework.</td>
</tr>
<tr>
<td><strong>15</strong></td>
<td>Intervention timed on the basis of biology of the invader and other related ecological parameters of the area - co-ordinate the seasonality of the treatment with the biology of the organism. Capture success may vary by season. Exploiting natural die-offs is wise.</td>
<td>(Genovesi 2001, Courchamp et al. 2003)</td>
<td>I agree and attempt to formalize this in my framework.</td>
</tr>
<tr>
<td><strong>16</strong></td>
<td>Timing should coincide with time of greatest availability - climatic variations can affect vulnerability (e.g., cold climate restrict access).</td>
<td>(Genovesi 2001)</td>
<td>I agree and attempt to formalize this in my framework.</td>
</tr>
<tr>
<td>17</td>
<td>When possible recovery of natural system after eradication</td>
<td>(Myers et al. 2000, Genovesi 2001, Vander Zanden et al. 2010)</td>
<td>I have not explicitly considered this in California; however it may be advisable to transplant native species after the eradication. The greater conservation concern is the protection of the greater San Francisco Bay from spreading populations from the marina.</td>
</tr>
<tr>
<td>18</td>
<td>Priority to new (immigrating) propagules [Mack and Lonsdale note that priority should be given to nascent loci]</td>
<td>(Genovesi 2001, Mack and Lonsdale 2002)</td>
<td>I do not suggest specific priority to immigrating individuals, but implicitly they must be treated. Immigration is a core consideration of my framework and I show how it can be overcome.</td>
</tr>
<tr>
<td>19</td>
<td>Priority to species thought to cause the most harm</td>
<td>(Genovesi 2001)</td>
<td>I do not consider selection of species as eradication targets. All else being equal this is reasonable, though.</td>
</tr>
<tr>
<td>20</td>
<td>[After establishment] priority to species that have caused reversible impacts – in other words target those species whose damage can be undone, rather than those whose damage is far-gone.</td>
<td>(Parker et al. 1999)</td>
<td>As above.</td>
</tr>
<tr>
<td></td>
<td>Description</td>
<td>Source</td>
<td>Notes</td>
</tr>
<tr>
<td>---</td>
<td>----------------------------------------------------------------------------</td>
<td>-------------------------</td>
<td>-----------------------------------------------------------------------------------------------------</td>
</tr>
<tr>
<td>21</td>
<td>Allee considerations - while it may not strictly be necessary to get all individuals due to population collapse, the level at which this may occur is unknown for most species.</td>
<td>Genovesi 2001</td>
<td>I do not dismiss Allee effects, but I ignore them in my analysis due to their notorious difficulty to study (Courchamp et al. 1999), and the uncertainty and risk of an eradication predicated on Allee effects</td>
</tr>
<tr>
<td>22</td>
<td>Social behavior affects vulnerability to removal</td>
<td>Genovesi 2001</td>
<td>This may not generalize to invertebrates. Likely not something that would decrease the efficacy of flame, but a valid point for more social animals.</td>
</tr>
<tr>
<td>23</td>
<td>Data demands: Minimum viable</td>
<td>Mack et al. 2000, Genovesi 2001</td>
<td>Not generally necessary. Studying this is difficult (see #21) and may retard action.</td>
</tr>
<tr>
<td>24</td>
<td>Data demands: the lag period (time between establishment and spread)</td>
<td>Genovesi 2001</td>
<td>As above.</td>
</tr>
<tr>
<td>25</td>
<td>Data demand: dispersal</td>
<td>Usher 1989, Bomford and O'Brien 1995, Genovesi 2001, Edwards and Leung 2009</td>
<td>All else considered equal, slow dispersers may be easier to eradicate. For formally, this research will be required in specific circumstances arising from comparison of treatment rates (see text) and has multiple scales of relevance.</td>
</tr>
<tr>
<td></td>
<td>Data demand: reproductive rate</td>
<td>(Genovesi 2001, Edwards and Leung 2009)</td>
<td>I agree. This is a critical piece of data for my framework.</td>
</tr>
<tr>
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<td>---------------------------------------</td>
<td>------------------------------------------------------------</td>
</tr>
<tr>
<td>27</td>
<td>Clearly defined roles of relevant agencies (incl. a lead agency)</td>
<td>(Myers et al. 2000, Anderson 2005, Shine et al. 2010)</td>
<td>Agreed. Co-ordination was maintained among relevant evaluative agencies (SERC, McGill, Loch Lomond)</td>
</tr>
<tr>
<td>28</td>
<td>Appropriate legal status for alien species i.e. to avoid unintended legal protection for invaders under measures applicable to higher taxa</td>
<td>(Shine et al. 2010)</td>
<td>I do not know the legal status of <em>Batillaria</em> in California but this would have to be investigated before eradication.</td>
</tr>
<tr>
<td>29</td>
<td>Consultation procedures to take account of socio-economic concerns e.g. commercial importance, customary/traditional uses, animal welfare issues</td>
<td>(Shine et al. 2010)</td>
<td>Consultation was very local and took place with marina staff and clients. Support for removal.</td>
</tr>
<tr>
<td>30</td>
<td>Consultation procedures with neighbouring states to support coordinated management and identify possible trans-boundary impacts of control techniques</td>
<td>(Shine et al. 2010)</td>
<td>N/A</td>
</tr>
<tr>
<td>31</td>
<td>Development of national IAS action plans – or incorporation of IAS into existing biodiversity action plans - to support coordinated management involving relevant public and private stakeholders</td>
<td>(Shine et al. 2010)</td>
<td>N/A</td>
</tr>
<tr>
<td>-----</td>
<td>-------------------------------------------------------------------------------------------------</td>
<td>----------------------</td>
<td>-----</td>
</tr>
<tr>
<td>32</td>
<td>Monitoring - Eradication (or even effective control) of invasive species requires repeatedly surveying the same area for survivors.</td>
<td>(Bax et al. 2001, Mack and Lonsdale 2002, Edwards and Leung 2009)</td>
<td>Follow-up monitoring is recommended. If re-invasion rate is assumed this isn’t required and periodic eradications can continue without explicit detection.</td>
</tr>
<tr>
<td>33</td>
<td>[Multiple passes] – <em>almost always require more than one treatment</em></td>
<td>(Edwards and Leung 2009)</td>
<td>The Loch Lomond snail system is an exception since treatment is so effective across age classes. This is likely why the original eradication pilot in 2006 failed.</td>
</tr>
<tr>
<td>34</td>
<td>Data demand: when did invader arrive</td>
<td>(Courchamp et al. 2003)</td>
<td>This is not generally required for eradication</td>
</tr>
<tr>
<td></td>
<td>Treatment – what is the best treatment?</td>
<td>(Courchamp et al. 2003, Anderson 2005, Edwards and Leung 2009, Brockerhoff et al. 2010)</td>
<td>This is a fundamental requirement and the first set of experiments I recommend. Flame was effective for <em>Batillaria</em>.</td>
</tr>
<tr>
<td>---</td>
<td>---------------------------------</td>
<td>-----------------------------------------------------------------</td>
<td>-----------------------------------------------------------------</td>
</tr>
<tr>
<td>36</td>
<td>Low reproductive rate</td>
<td>(Brockerhoff et al. 2010)</td>
<td>This may reduce the required effort (and thus decrease cost), but is not a pre-requisite for eradication.</td>
</tr>
<tr>
<td>37</td>
<td>Clear objectives of eradication</td>
<td>(Bax et al. 2001)</td>
<td>In California my fundamental goal is simply removal and does not specifically include restoration or other goals.</td>
</tr>
<tr>
<td>38</td>
<td>Contingency plan for R.R.</td>
<td>(Genovesi 2001)</td>
<td>I agree. This should take the form of considering re-eradication if re-invasion is likely. May require long-distance dispersal research.</td>
</tr>
<tr>
<td>39</td>
<td>[Eradications are more likely in] Man-made habitats</td>
<td>(Pluess et al. 2012)</td>
<td>This is in support of eradicating <em>Batillaria</em>.</td>
</tr>
<tr>
<td>40</td>
<td>Pathogens, bacteria and viruses most likely to be eradicated, fungi least, plants and invertebrates intermediate</td>
<td>(Pluess et al. 2012)</td>
<td>Moderate support for eradicating <em>Batillaria</em></td>
</tr>
</tbody>
</table>
Stakeholder involvement (i.e., those affected by the eradication) (Anderson 2005)
The marina staff was supportive throughout my research.

Risk assessment for other possible infested sites (Anderson 2005)
I agree. This is subsumed within meso-scale immigration research.

Local: stakeholders, resources, and expertise. Andersen felt most eradinations were “bottom-up” efforts demanding local involvement. (Anderson 2005)
My work may not be an excellent example of this.

Table B.3: A table of the 43 eradication guidelines found in published literature.
References


Parker, I. M., D. Simberloff, W. M. Lonsdale, K. Goodell, M. Wonham, P. M.
Kareiva, M. H. Williamson, B. Von Holle, P. B. Moyle, J. E. Byers, and L.
Goldwasser. 1999. Impact: toward a framework for understanding the
ecological effects of invaders. Biological Invasions 1:3-19.

Pluess, T., V. Jarošík, P. Pyšek, R. Cannon, J. Pergl, A. Breukers, and S.
Bacher. 2012. Which factors affect the success or failure of eradication


Shine, C., M. Kettunen, P. Genovesi, F. Essl, S. Gollasch, W. Rabitsch, R.
Scalera, U. Starfinger, and P. ten Brink. 2010. Assessment to support
continued development of the EU Strategy to combat invasive alien
species. Final Report for the European Commission. Institute for European
Environmental Policy, Brussels, Belgium.

Simberloff, D. 2003. How much information on population biology is needed to

Usher, M. B. 1989. Ecological effects of controlling invasive terrestrial
vertebrates. Pages 463-484 in J. A. Drake and H. A. Mooney, editors.
Appendix C

A team is assigned an area that they must treat during a tide cycle. I call this area a wedge (Figure C.1), it runs from the water line at MLLW+1ft of tidal elevation \((z_L=1\text{ft}; \text{Figure } C.1)\) to the top of the intertidal \((z_H; \text{Figure } C.1)\). The wedge comprises one or more different substrate types \((M_{1-3}; \text{Figure } C.1)\). The wedge is subdivided into slivers 1m wide along the \(w\)-axis (light grey lines; Figure C.1). Areas of distinct sediment type delimited by slivers are called cells (as an example, one cell is shaded dark grey in Figure C.1). The water line rises and falls according to the tidal cycle on the \(z\)-axis moving a horizontal line up and down the \(d\)-axis. The width of wedge that can be treated by a team on a given day, \(w\), depends on the duration of the tidal cycle on the day which the treatment is conducted, the size of the team, and the length of treatment required for each substrate type present within the wedge.

Treatment of a wedge must follow the tide as it recedes and exposes cells. This work will be conducted in segments – sections of the wedge that run the entire extent of the wedge on the \(w\)-axis (in Figure C.2b segment 0 is shaded grey). The upper and lower bounds of each segment on the \(d\)-axis are delimited by highs and lows of any cells in the wedge. Visually, this time at which the tide reaches the upper or lower edge of the segment is where the tidal elevation
curve (Figure C.2a) intersects the horizontal line delimiting the segment (spanning Figure C.2 a-b). The intersection on the left of figure C.2 is when the segment is first exposed; the next intersection to the right is when the segment begins to be covered again. Mapping the tops and bottoms of the segments to the tidal graph I can calculate how long each segment will be exposed. Segment 1, for example, is first exposed when the tide is at 5.1ft (1.55 m) and begins to be covered again when the tide returns to 4.2 ft (1.42 m). The time this takes is shown on the time axis below Figure C.2a as the difference between $t'_1$ and $t''_1$. The lower-most segment bounded by $z_L=+1ft$ is exposed only briefly so it is important for the team to treat it with priority.

The team should follow the receding tide downward treating each segment for $t'_{i+1} - t'_i$ minutes – that is treating each segment until the next segment is revealed by the tide. This may leave some segments incompletely treated but the team can return to them later. Once the team reaches the last segment they must treat it completely before the tide returns to cover it. Assignment of wedges must be made to ensure this is possible. Treatment of a segment can be completed in $T_N$ minutes,

\[
T_N = \sum_{j=0}^{J} R_j C_j \frac{P}{P} \quad \text{C.1}
\]
where \( R_j \) is the per person treatment rate for each of the \( j \) cells that is overlaid by the segment, \( c_j \) is the fraction of that cell's area that is covered by the segment and \( P \) is the number of people in the team. The team will have \( t''_N - t'_N \) minutes to treat the segment. The team can then work their way back up the wedge, ahead of the returning tide, completing the segments that had not yet been finished, in order. If the team is able to complete this effort before the tide covers the segments the team is able to treat this wedge. The ability of a team to treat a wedge depends on the number of members on the team, \( P \), the tide cycle on the day of the year they are working, the size of the wedge and the pattern of sediment types within the wedge.

The above is formalized by the following conditional:

\[
t''_i - \left( t'_N + T_N + S + \sum_{j=1}^{N-1} T_j - (t'_{i+1} - t'_j) \right) \geq 0
\]

The variables \( t'_i \) and \( t''_i \) are the beginning and end times of the exposure of segment \( i \) and are dependent on the tides on the day being considered. \( t'_i \) is defined as the time at which the receding tide reaches the upper edge of cell \( i \), and \( t''_i \) is conservatively defined as the time at which the tide returns to the lower edge of cell \( i \). Since the team must deploy a barrier to isolate the wedge, I include a spin-up time, \( S \) per day. I assume that there are barriers set up on one side of each wedge (re-using the barrier on the other side from the previous day's effort).
and that they can be deployed even during high tide (by boat). I modeled per-person barrier set-up time as \(1/P\) relationship, assuming each person contributes an identical amount of help to some fixed minimum, \(m\) and from some maximum single-person setup time \(M\).

\[
S = P \left( \frac{M}{P} + m \right) = M + Pm
\]  

C.3

A team working on a day with a very low tide would have more time to work and would be able to treat a larger wedge. A larger team would be able to treat a wedge faster in a given amount of time and similarly would be able to treat a larger wedge on a given day. From a given starting day I can simulate a fixed size team working on each day with sufficiently low tides and each day solve the size of the next wedge they can treat. In my analysis a team starts on the eastern side of the mouth of the marina and works their way around the entire marina treating one wedge per day, working only on days with appropriately low tides. Each day the team treats the largest wedge possible according to equation C.2. The team tiles together wedges until they have treated the entire marina. This generates a day-by-day schedule of where and when the team will be working in addition to a final measure of feasibility for a given team size and a total amount of time and effort spent.
Calculations were generated for teams of 1, 2, 4, 8, 15, 30, 57, 111, 214, and 414 people with start days on each valid working day between January 1, 2012 and December 31, 2022. Valid days were those with tides below 1ft during working hours (8am-5pm). For each combination of people and start day I calculated: i) whether or not the eradication would be possible before the end day of December 31, 2022, ii) the total time to complete the program (taken as end day minus start day), iii) the total effort in units of people \times hours, and iv) a day-by-day eradication schedule indicating where the team would work on what days, and for how long.
Figure C.1: A “wedge” of the intertidal to be treated for *Batillaria attramentaria*.

The z axis depicts the vertical axis. \( z_L \) and \( z_H \) are low and high tide lines, \( M_{1-3} \) denote different substrate types (with different treatment rates), the length of the w axis for a given day and team size may be calculated using equation C.2.
Figure C.2: A diagram showing the relation between the tide and the exposure of different levels of the intertidal wedge. The tidal plot may be used to show visually the amount of time a cell is exposed by the tide.