



Optimizing early detection of non-indigenous species: Estimating the scale of dispersal of a nascent population of the invasive tunicate *Ciona intestinalis* (L.)

Samuel B. Collin^{a,*}, Paul K. Edwards^b, Brian Leung^b, Ladd E. Johnson^a

^a Université Laval, Quebec City, QC G1V 0A6, Canada

^b McGill University, Montreal, QC H3A 0G4, Canada

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ABSTRACT

Knowledge of dispersal and establishment during the early stages of invasion is essential for allocating monitoring effort, detecting nascent populations and predicting spread. The scarcity of these data, however, provides little guidance for monitoring programs. Here we present data on the adult distribution and the subsequent pattern of larval recruitment from a nascent population of the invasive tunicate *Ciona intestinalis* in Prince Edward Island, Canada. Existing niche models indicate the entire study site is suitable for recruitment, suggesting an equal probability of detection throughout the site. In contrast, we found a heterogeneous pattern of larval recruitment, including areas of zero recruitment. By fitting a dispersal kernel, we show *Ciona* is not capable of naturally dispersing between bays, restricting further spread, and provide guidance for future monitoring. Our results also highlight how large-scale models, although important, lack the small-scale patterns essential for monitoring and early detection of invasive species.

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1. Introduction

Non-indigenous species (NIS) have created serious challenges for ecosystem conservation and human industries across the planet (Mack et al., 2000; Hooper et al., 2005). The impacts of NIS are highly variable and unpredictable, but such is the potential for ecological and economic harm that there is great interest among ecologists to prevent the establishment and spread of NIS (Pimental et al., 2000; Occhipinti Ambroggi and Sheppard, 2007). The invasion process is often considered to consist of four stages: (1) transport and introduction; (2) local establishment; (3) regional spread; and (4) population growth to nuisance levels (MacIsaac et al., 2002; Lockwood et al., 2005). Intervention at the first stage is obviously the best strategy because once established, eradication or control of NIS is costly at best or impossible at worst (Myers, 2000). Still, in spite of efforts aimed at preventing transportation of potential invasive species, introductions continue to occur (Lodge et al., 2006). Unfortunately, the subsequent stages of such invasions (i.e., local establishment and spread) usually pass unnoticed due to a lack of effective monitoring programs (Kraft and Johnson, 2000; Vander

Zanden and Olden, 2008). Such programs are critical as they can provide information at a variety of levels, including patterns of invasions (e.g., identification of vectors and invasion “hotspots”) and rates of range expansion. Most importantly, early detection can provide a first warning of an initial invasion and offers the best opportunity for any possible eradication efforts as populations are both small and localised (Simberloff et al., 2005). Moreover, identification of nascent populations is important for controlling NIS by detecting and suppressing fringe populations (Moody and Mack, 1988), thereby slowing the rate of spread (Sharov et al., 1998) and improving the efficacy of preventative measures (e.g., quarantines). Studying the transitional phase between introduction and establishment can thus provide key information for management, especially if new NIS can be detected early.

Although conceptually a simple idea, the early detection of nascent populations is inherently difficult, and the temporal window between introduction and widespread dispersal can be short, adding additional pressure on monitoring strategies. These same factors have also made research in this area difficult, and thus there is a paucity of studies conducted during these early stages (Marsico, 2010). In the simplest terms, the problem is one of sampling. There are two basic aspects to any monitoring effort: the overall effort (e.g., number of samples) and the design of the sampling effort (i.e., the spatial and temporal distribution of effort). With regard to the former, more effort creates a greater probability of detection, but with obvious associated costs. The latter is less obvious and requires knowledge of both the likely time and location of introductions. However, it is

* Corresponding author. Address: Université Laval, Département de Biologie, 1045, av. de la Médecine, Québec, QC G1V 0A6, Canada. Tel.: +1 (418) 656 2131x14715.

E-mail addresses: samuel.collin.1@ulaval.ca (S.B. Collin), paul.edwards1@mail.mcgill.ca (P.K. Edwards), brian.leung2@mcgill.ca (B. Leung), ladd.johnson@bio.ulaval.ca (L.E. Johnson).

unlikely that the initial colonists will arrive in numbers sufficiently high to be detected, and thus most monitoring efforts functionally focus on detecting the subsequent first generations (e.g., Kraft and Johnson, 2000; Hayes et al., 2005). Although much literature focuses on searching where initial introductions are most likely to occur (see review by Campbell et al. (2007)), knowledge of the intergenerational dispersal of propagules becomes essential information for optimizing the sampling design, especially when points of potential introduction are known or suspected.

In aquatic systems, the unintentional introduction of most NIS occurs through a limited number of vectors, principally through shipping, boating and aquaculture activities. Although introduction can occur while vectors are in transit (e.g., sloughing of hull-fouling organisms, release of ballast water) or through less predictable vectors of secondary spread (e.g., recreational boating; Kelly et al., 2013), the principal vectors typically operate at or from specific locations (e.g., ports, boat launches) and thus, the possible points of introduction are generally well known. Natural dispersal is often considered an unmanageable vector (Kanary et al., 2011), but if the dispersal potential is known, sampling stations can then be positioned at appropriate distances away from suspected points of introduction. However, patterns of dispersal are, in reality, very poorly known, even for sessile benthic organisms due to the small size of the dispersive larval stage (but see Olson, 1983; Stoner, 1992). From a theoretical standpoint, dispersal should assume a kernel function (e.g., integro-difference models, Kot et al., 1996) that describes patterns of recruitment in relation to the location of the adult population. This approach has been successfully used in landscape ecology to model dispersal in plants (Fitt et al., 1987) and insects (Roques et al., 2008), albeit usually over large spatial scales (Siegel et al., 2003). However, it is not clear how applicable these techniques are when working in the marine environment or at the finer spatial scales over which the dispersal of some newly-introduced AIS typically occurs. Moreover, the extent to which water motion (e.g., tides, currents) influences the distribution of propagules is unknown (but see Kanary et al., 2011). For effective monitoring, it is thus essential to know the scales of effective dispersal (i.e., the range of dispersal) as well as the degree and predictability of any heterogeneity within that range in order to appropriately assign sampling effort. Otherwise, sampling will be haphazardly assigned (i.e., no guidance from predictable heterogeneity in recruitment within the dispersal range) or take place at too large a scale (i.e., outside the dispersal range).

To investigate the importance of dispersal when designing monitoring strategies for NIS, we studied the very early stages of invasion (1 year after known introduction) of a known problematic invasive tunicate, *Ciona intestinalis* (Lambert and Lambert, 1998; McDonald, 2004; Robinson et al., 2005; Uribe and Etchepare, 2002; Howes et al., 2007), hereafter after referred to as *Ciona*, in Prince Edward Island (PEI), Canada. *Ciona* is of particular importance in PEI as it heavily fouls local aquaculture facilities, creating additional costs to mussel farming practices (Thompson and MacNair, 2004). A large-scale species distribution model (SDM) for *Ciona* has already been applied to Canadian waters (Therriault and Herborg, 2008), which identified the eastern and northern coastlines of PEI as at-risk from *Ciona* invasion based upon temperature, salinity, dissolved oxygen and chlorophyll *a* data. Although this work correctly predicted the eastern coastline of PEI as at-risk (*Ciona* was first detected in Brudenell river, eastern PEI in 2004 (Locke et al., 2007) and has since spread to adjacent bays), it provides little in terms of guidance for managers monitoring for *Ciona* within this region or elsewhere. Without further knowledge on the dispersal range and patterns of recruitment, monitoring efforts will be poorly allocated and lack the accuracy required for early detection.

In this study we used information on the distribution of a small adult population and subsequent larval recruitment within a small

bay in eastern PEI to investigate the dispersal potential and patterns of recruitment of *Ciona*. Using these data we assess the problems associated with monitoring allocation at small scales and offer guidance on key dispersal characteristics of *Ciona* to future monitoring programmes in areas at risk of invasion by *Ciona*. At present there are other similar bays within the same at-risk region that are not invaded and, therefore, information to guide the design of monitoring programs is required. More generally, we feel our approach can be applied not only to other species of tunicates but to other invasive species as well.

2. Methods

2.1. Study site

Fieldwork was conducted on the eastern coast of PEI in Boughton River, which, despite its name, is a small semi-enclosed bay, approximately 6 km in length, widening from west to east (maximum width ~2 km) but with only a small entrance (approximately 100 m wide) to the open sea (Fig. 1). *Ciona* was first detected in Boughton River in the fall of 2007 (2 recruits, G. Arsenault, pers. comm.), which provided a rare opportunity to collect high-resolution recruitment data during the very early stages of an invasion. The water regime within the bay is governed by a semi-diurnal tidal system (tidal period of approximately 12 h), which creates a bi-directional, east–west water flow within the bay. Towards the mouth of the bay, current flow follows a man-made channel that navigates a shallow region towards the middle of the bay. However, west of this shallow region, the cross-section of the bay is more typical of a river cross-section, with deeper water found in the middle of the bay. Due to the frequency of tidal changes (every 6 h) and the larval planktonic duration of *Ciona* (minimum of 24 h), we expected larvae to be exposed to several tidal changes and thus be fairly diffused throughout the bay.

Temperature and salinity data (collected on 22 Aug 2012 within the bay using an SBE 19plus V2 Seacat CTD Profiler at 2-m depth) ranged from 20.5–24.4 °C (mean = 22.2 °C) and 25.4–27.7 ppt (mean = 27.1 ppt). Both of these ranges fall well within the published temperature (–1–30 °C) and salinity (12–40 ppt) tolerances of adult *Ciona* (Dybern, 1965, 1967; Carver et al., 2006; Therriault and Herborg, 2007), indicating the entirety of Boughton River was suitable for *Ciona* recruitment. The general pattern for temperature was an increase towards the western end of the bay, away from the mouth of the bay, and salinity values showed the opposite trend with higher values to the east. However, the profiler casts also indicate that freshwater input from surface runoff was minimal, affecting only the top meter of the water column in the western end of the bay. There were no obvious effects of freshwater input in the main body of the bay or at the 2-m sampling depths.

The natural substrata in Boughton River is predominantly sand and silt, which are unsuitable for *Ciona* – therefore *Ciona* was only observed on artificial substrata, as is seen generally in PEI (Locke et al., 2007). The majority of suitable artificial substrata in Boughton River is provided by the mussel aquaculture facilities (i.e., “leases”, including anchors, buoys, lines, and mussel “socks”) located in the centre of the bay, a small loading dock towards the west, and a small harbour near the entrance of the bay (Fig. 1). The limited substrata available for settlement constrained the possible locations for colonization, which improved our ability to locate and map the adult population.

2.2. Adult survey

Underwater surveys were performed in 2008 to map the distribution of the adult population on mussel leases. Thirty-three

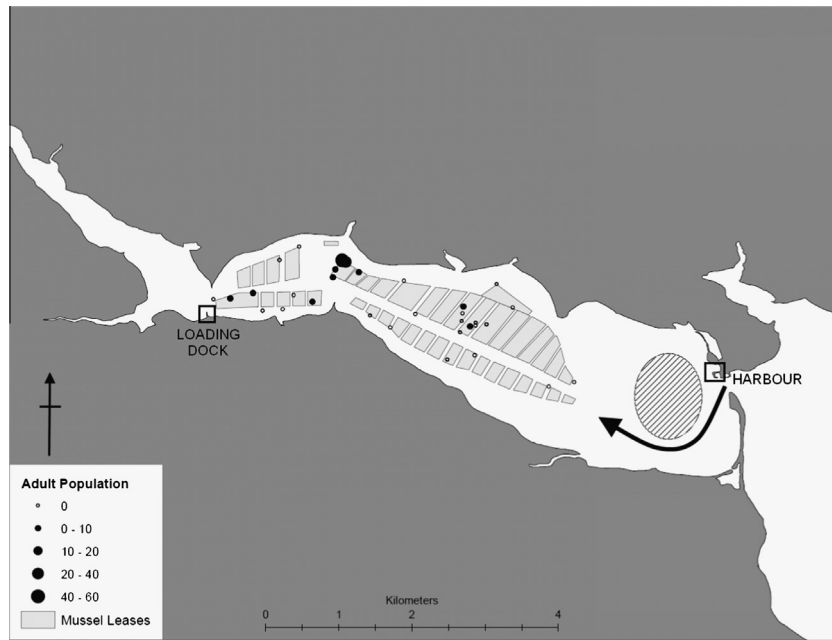


Fig. 1. Distribution of adult *Ciona intestinalis* in Boughton River (Prince Edward Island, Canada) in June 2008 based on 50-m underwater surveys ($n = 33$). Larger circles represent larger populations and clear circles represent an absence of adults. Light grey rectangles within the bay represent mussel leases, the scored area represents a shallow region (1–2 m depth), and the black arrow signifies the man-made channel.

surveys were conducted in June before *Ciona* normally becomes reproductively active (Ramsay et al., 2009) and thus documented the distribution of the first reproductively-active adult population of the year. Each survey consisted of a 50-m transect within a mussel lease surveyed by two divers starting from a haphazardly-chosen location. Each transect ran horizontally through the water following rows of vertically-hung mussel socks, which were completely inspected, including the natural substratum below the mussel lines. The total number of *Ciona* present was recorded by both divers, and the two counts averaged. If mussel leases had recently been harvested (i.e., mussel socks removed), 50 m of the remaining *in situ* equipment (e.g., ropes, buoys and anchor lines) was surveyed.

2.3. Patterns of larval recruitment

Unlike previous studies using SDMs where different habitats were surveyed (e.g., Inglis et al., 2006), we deployed a large grid of quasi-systematically-placed settlement plates (88 stations) at a constant depth (2 m) to collect recruitment data. Plates were deployed for 2 weeks beginning on 8 Aug 2008 both within and outside of the mussel leases (Fig. 2). Each station contained a 20×20 cm² PVC settlement plate (roughened with #50 sandpaper to enhance settlement) suspended horizontally from a surface buoy and anchored to the bottom by a 9-mm polypropylene cord attached to a cement block; an intermediate weight kept the top half of the line vertical and thus the plate horizontal. After collection, the plates were transported to the laboratory in seawater and the total number of larvae settled on the underside of each plate counted using a stereomicroscope at $40\times$ magnification within 48 h of collection.

2.4. Dispersal model – kernel fitting

Dispersal kernels describe the probability of dispersal of propagules at different distances from adult sources (Nathan, 2006). To determine if the pattern of larval recruitment could be modelled as a function of distance and adult population size, we fit

$$P_j = c \sum_{i=1}^{|A|} A_i f(d_{i-j}; \bar{v})$$

where P_j is the recruitment on plate j , c is a fecundity scalar, $|A|$ is the total number of adult populations in the whole bay, A_i is the size of the adult population i , d_{i-j} is the distance between plate j and adult population i and \bar{v} is the vector of free parameters to the function $f(d)$. For the function $f(d)$ we used the Weibull distribution, as it has a very flexible shape that may approximate a variety of dispersal kernels (Morales and Carlo, 2006), including both hump-shaped and exponential decay shapes. The c and v parameters were fit automatically using R (R Development Core Team, 2012). We used bootstrapping to generate the 95% confidence intervals for the fit parameters. From the original set of sampling stations, we drew 10,000 random subsamples with replacement. We refit the kernel parameters for each random subset to generate a distribution of fit parameters.

3. Results

3.1. Adult distribution

Ciona was observed in 10 of the 33 surveys with a mean number of 2.5 ± 1.4 (S.E.) per transect, with a maximum of 40. Although *Ciona* was present in several locations, the highest densities were found to be concentrated in the northern part of the bay (Fig. 1). *Ciona* were never observed on the natural substrata within and surrounding the mussel leases.

3.2. 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 (S.E. = 1.0) per plate, with a maximum count of 49. Recruits were found on all but 4 of the 63 stations located within the mussel leases and on all 6 stations located west of the leases. In contrast, *Ciona* was present on only one of the 13 stations east of the mussel leases, i.e., towards the mouth of the bay. Overall

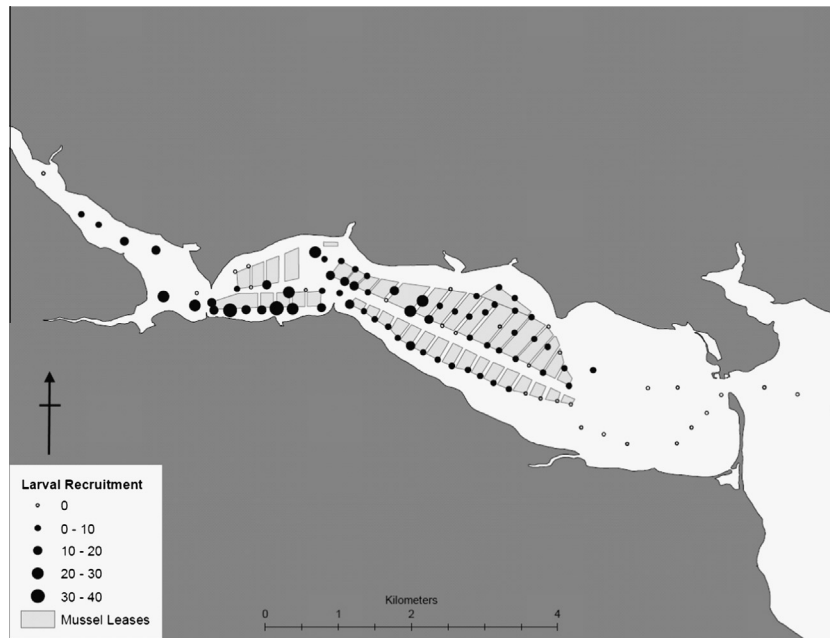


Fig. 2. Pattern of *Ciona intestinalis* larval recruitment on the 88-station grid of settlement plates in Boughton River, Prince Edward Island, Canada. Settlement plates (400 cm²) were deployed on 8 August 2008 for 2 weeks. The size of the circle increases with larger counts of larvae/plate, and clear circles represent zero recruitment. Grey rectangles within the bay represent mussel leases.

the pattern of recruitment was found to be heterogeneous (Global Moran's $I = 0.266$, $P = <0.01$), with higher levels of recruitment generally occurring towards the western end of the bay (Fig. 2).

3.3. Dispersal model – kernel fitting

The Weibull distribution fit the recruitment data (parameters $c = 0.33 \pm 0.0006$, $\lambda(\text{scale}) = 1.75 \pm 0.0038$ and $k(\text{shape}) = 1.39 \pm 0.0019$). The overall fit was good with a Pearson r of 0.64 (Fig. 3). The fitted Weibull function showed that larval recruitment was not highest close to adult populations, but peaked at a distance of 0.86 km (Fig. 4) with 95% of the recruitment occurring within 3.8 km from the source.

4. Discussion

The dispersal of tunicates is widely believed to be limited due to their short planktonic period, and the dispersal kernel derived from our data demonstrates clearly that *Ciona's* dispersal range is limited to just a few kilometres. More surprising is the successful fitting of the Weibull function which, in contrast to the commonly-assumed negative exponential decay curve (Kot et al., 1996), highlights how patterns of recruitment can take unexpected forms, i.e., the lack of recruitment near adult source populations. From a management perspective, sampling at mid-range distances (~1 km), rather than close to the adult source, would thus be more effective for detecting invasions. The shape of the dispersal kernel can be attributed to certain characteristics of *Ciona's* life cycle. *Ciona* is an external fertilizer, and therefore there can be time lags between egg release (up to 30 h (Svane and Havenhand, 1993)), fertilization (24 h to become competent (Berrill, 1947)) and settlement, which would result in low levels of settlement close to adults. Overall, estimates of the dispersal period after larvae become competent range from a few hours to 6 d (Svane and Havenhand, 1993), but generally settlement is thought to occur at the shorter end of this scale – minutes–hours (Berrill, 1947; Svane and Havenhand, 1993), which would explain the peak in settle-

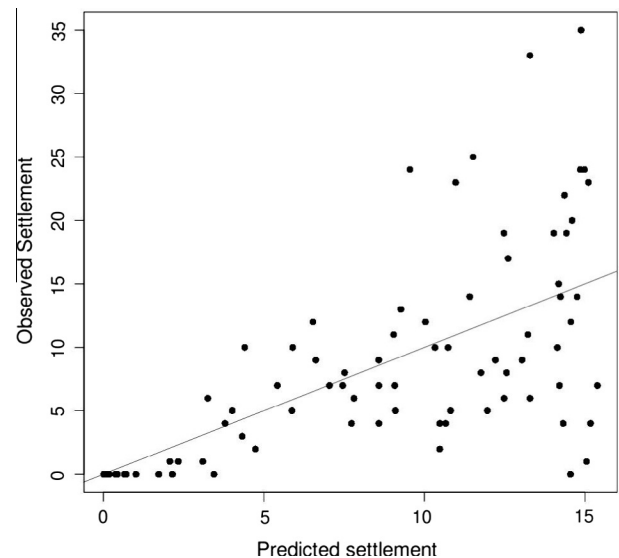


Fig. 3. Predicted settlement vs. observed settlement fitting of Weibull dispersal function (Pearson's $r = 0.64$) for *Ciona intestinalis* larval recruitment, using adult surveys and larval recruitment data in Boughton River (Prince Edward Island, Canada).

ment around 1 km. The high temperatures recorded in Boughton River, between 20 °C and 24 °C could shorten the development process (Svane and Young, 1989), which would also contribute the 1-km peak and the limited dispersal range.

Ciona's dispersal potential is too short for inter-bay dispersal in PEI, since bays are typically separated by distances of 10 s of km, suggesting the recent spread between bays was most likely human-mediated, e.g., aquaculture activity and/or recreational boating (Darbyson et al., 2009). These findings may seem intuitive after the fact, but these data have not been available to managers in a practical format. Had they been made available earlier, local managers could have acted more promptly in containing *Ciona* once it had first been detected by controlling human activities to prevent

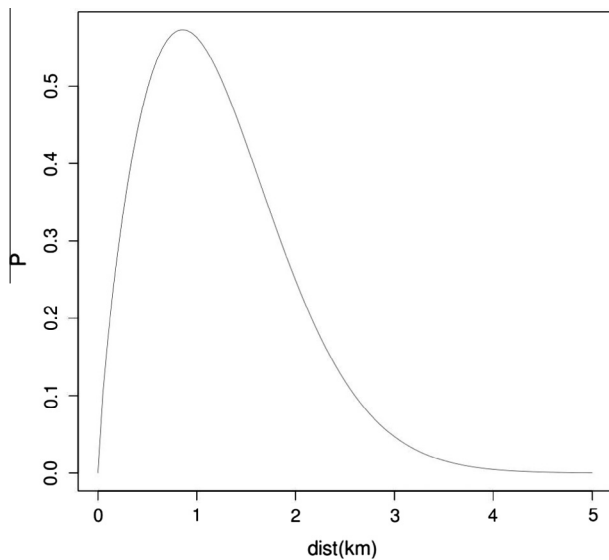


Fig. 4. Weibull function dispersal kernel fit to *Ciona intestinalis* larval recruitment based on values of larval recruitment with distance from adult populations in Boughton River (Prince Edward Island, Canada). “P” represents the proportion of settling larvae.

further spread to adjacent bays outside of the natural dispersal range (Gertzen and Leung, 2011; Clarke Murray et al., 2011). This applies not only to *Ciona* but to other species of invasive tunicates in PEI and likely elsewhere.

The over-dispersion of data in the Weibull observed-vs.-predicted plot (Fig. 3) is indicative of un-modelled predictors (Hilbe, 2007) and suggests that the simple, symmetrical distance from adults is not the only factor driving the pattern of recruitment. Our standardised sampling method reduced the influence of other likely environmental factors (e.g., substratum, depth), but other unidentified factors may have influenced recruitment patterns. The shape of the bay and tidal regime suggest that east–west water movement may be greater than north–south, though our dispersal kernel implicitly assumes symmetry. Other dynamics, such as turbulence and random diffusion will contribute to some north–south movement but, nonetheless, elongation of dispersal along the east–west axis may account for some of the over-dispersion of data. Despite this, the fit of the Weibull function is still remarkably good and captures well the dispersion of larval recruitment.

The small size of Boughton River, the planktonic larval duration of *Ciona* (<1–6 d) and the frequently changing tides might be expected to lead to a widespread dispersal of larvae throughout the bay. In spite of these homogenising factors, a signal of the adult population was seen clearly in the distribution of recruitment. Not only did we find a heterogeneous pattern of recruitment, we also found regions of zero settlement within the bay, which was surprising given the long deployment time of the settlement plates (2 weeks). We suspect that circulation might have contributed significantly to the unexplained variation we observed. For example, the general lack of settlement in the eastern end of the bay could have been caused by changes in water direction and current magnitude created by the channel, the shallow area, and the outlet to the sea. It is also possible that the current speeds in the eastern end of the bay are too high for larval settlement (Abelson and Denny, 1997). Regardless, our intention here was to minimise the effect of environmental variation (e.g., standardised plates at a fixed depth) to characterise dispersal patterns statistically, and not to determine the precise mechanisms underlying them. At a larger scale, there is likely some larval dispersal outside of the bay similar to that predicted by Canary et al. (2011) elsewhere in PEI and observed by Petersen and Svane (1995) in Denmark. How-

ever, unfavourable conditions and low densities (i.e., Allee effects (Courchamp et al., 1999)) will undoubtedly limit the establishment of new populations and thus secondary spread.

The SDM approach applied by Therriault and Herborg (2008), one that has been effective in both aquatic and terrestrial systems (Peterson and Vieglais, 2001; Thuiller et al., 2005; Inglis et al., 2006; Trebitz et al., 2009), successfully identified regions at risk in Canada, but the resolution was far too large to capture the variations in recruitment observed within this study. A key problem with the SDM approach for early detection of invasive species is that it is static in nature, with dispersal generally not considered limiting, and assumes species presence in *all* potential habitats suitable for recruitment. This assumption may be appropriate for species that are in ecological equilibrium and widely dispersed, i.e., native or well-established invasive species, but during the early stages of invasion, nascent populations are usually small and isolated, occupying only a small portion of suitable habitat available (Rouget and Richardson, 2003). For example, prior to this study, it would have seemed reasonable to place a monitoring station anywhere in Boughton River but, even in this small and simple bay, recruitment is highly variable, and poorly-placed monitoring stations could return a false negative result. Therefore, the uses of large-scale predictions alone may not be accurate enough to effectively guide the detection of nascent populations.

The most effective method for monitoring would be to use the larger-scale SDM and the smaller-scale dispersal kernel approaches in tandem to identify locations that are both highly suitable to a given NIS (environmental aspect) and likely to receive a high number of propagules (dispersal aspect). However, a limitation exists in that SDMs are based upon the ecology of adult stages (e.g., environmental tolerances), whereas for many AIS, such as *Ciona*, monitoring targets the planktonic larvae stage, which can have different environmental constraints. Larval behaviour is influenced by a variety of environmental stimuli (Crisp, 1961; Olson, 1983; Pawlik, 1992; Rodriguez et al., 1993; Abelson and Denny, 1997; Kingsford et al., 2002), which occur on very small scales and cannot be accurately captured at large scales. Therefore, using environmental tolerance estimates from adult distributions to design detection strategies that target the dispersive larval stage may be misleading, and where possible, monitoring strategies need to integrate multi-scale analyses that incorporate both life stages.

We were fortunate in discovering this invasion in its earliest stages as the patterns of recruitment within the bay became less clear over time (Collin, 2013). However, it only represents a single observation of early larval recruitment, driven by an isolated adult population. Thus, extrapolating our result to other systems could be misleading, especially for other taxon and other coastal conditions. Moreover, even for the particular species examined here, the patterns could vary spatially and temporally. We feel nevertheless that without further information, it still provides a useful starting point for similar situations (e.g., another embayment in PEI). Clearly, additional such studies are needed and strongly encouraged as replication is needed for validating the specifics of this situation as well as exploring applications to other systems.

Our study demonstrates how a small-scale approach can complement the larger-scale guidance currently available. Large-scale surveys that identify and prioritise areas at risk (i.e., SDMs) are essential but should be considered as a preliminary filter. The next logical step is to pinpoint the most likely sites of introduction and, working on a more local scale, assess the suitability of the surrounding environment. Finally, this information needs to be coupled with an understanding of the life history and dispersal potential of the focal species to identify the appropriate scale for monitoring in order to optimise the allocation of sampling efforts, especially when targeting propagules produced by a nascent population (e.g., Kraft and Johnson, 2000). It is essential then for

managers to recognise that by incorporating multi-scale approaches to surveillance and monitoring, coupled with behavioural and dispersal characteristics, the early detection of nascent populations of nuisance species becomes a more realistic objective in the management of biological invasions.

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