

An empirical probability model of detecting species at low densities

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Abstract. False negatives, not detecting things that are actually present, are an important but understudied problem. False negatives are the result of our inability to perfectly detect species, especially those at low density such as endangered species or newly arriving introduced species. They reduce our ability to interpret presence–absence survey data and make sound management decisions (e.g., rapid response). To reduce the probability of false negatives, we need to compare the efficacy and sensitivity of different sampling approaches and quantify an unbiased estimate of the probability of detection. We conducted field experiments in the intertidal zone of New England and New York to test the sensitivity of two sampling approaches (quadrat vs. total area search, TAS), given different target characteristics (mobile vs. sessile). Using logistic regression we built detection curves for each sampling approach that related the sampling intensity and the density of targets to the probability of detection. The TAS approach reduced the probability of false negatives and detected targets faster than the quadrat approach. Mobility of targets increased the time to detection but did not affect detection success. Finally, we interpreted two years of presence–absence data on the distribution of the Asian shore crab (*Hemigrapsus sanguineus*) in New England and New York, using our probability model for false negatives. The type of experimental approach in this paper can help to reduce false negatives and increase our ability to detect species at low densities by refining sampling approaches, which can guide conservation strategies and management decisions in various areas of ecology such as conservation biology and invasion ecology.

Key words: Asian shore crab; bioinvasion; *Carcinus maenas*; coastal New England and New York, USA; detection; European green crab; false negatives; *Hemigrapsus sanguineus*; marine introduced species; presence–absence survey data; sampling approach; search theory.

INTRODUCTION

Bioinvasion is a form of global change that is homogenizing the biota of terrestrial and aquatic environments (Ricciardi 2007). Marine environments are no exception, as they are heavily invaded and colonization by new introduced species continues (Grosholz 2002, 2005). Despite its importance and recent progress, marine invasion biology still lags behind its counterparts in terrestrial and freshwater ecosystems, and, arguably, only started as a formal field of science in the 1970s (Carlton 1979, Ruiz et al. 1997, Grosholz 2002). Progress in this field, especially in our ability to manage marine introduced species, has been hindered by real-world limitations such as insufficient resources (e.g., funding, personnel, and equipment to extensively monitor vast areas), limited data, and an inability to perfectly detect organisms (Bax et al. 2001, Lodge et al. 2006). These problems are not ephemeral, so invasion biologists need to address them to achieve a central objective: more effective monitoring and management of

invasive species to avoid significant economic, ecological, and/or human health consequences (Carlton 2001).

Monitoring is an important precursor to effective management of invasive species. For instance, detection of bioinvaders at an early stage, when the population is localized and at a low density, will maximize the probability of successful eradication (Rejmanek and Pitcairn 2002). Introduced species often remain undetected or are only detected years after the initial introduction, when the population size is large and its distribution is already widespread (Geller et al. 1997). In the applied field of invasion biology, early detection can be the difference between successful eradication, which means a one-time investment of money and personnel, or the costly establishment of an invasive species and the perpetual investments for control efforts. Optimal sampling approaches that minimize the probability of false negatives are vital to maximizing the success of monitoring efforts.

The ability to detect new invaders will be strongly affected by the monitoring approach used and the biological characteristics of the species. For instance, the random quadrat approach is arguably one of the most common sampling approaches (Chiarucci et al. 2003); it can provide data on population structure (Wernberg 2009), abundance (Rueda and Salas 2008), and diversity

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of an ecosystem (Liuzzi and Gappa 2008), and is often used for monitoring and detection (Hewitt and Martin 2001, Robinson et al. 2004, Delaney et al. 2008). Although this approach is useful for monitoring newly introduced species, it arguably falls short; it underestimates the presence of organisms at low abundance (Miller and Ambrose 2000). In contrast, it may be far simpler and more effective to perform a total area search (TAS), a modified time transect search of an entire area, rather than along a single line and not be constrained to searching small, restricted areas defined by quadrats. The trade-off is that the TAS approach covers more area whereas the quadrat approach searches less area but in greater intensity and completeness. Further, there may be an interaction with species characteristics such as mobility. Motile organisms might be more difficult to detect than sessile organisms because they can hide from searchers, as they do from predators, and this may differentially affect the efficacy of alternative sampling approaches. Alternatively, mobility might increase the probability of detection by alerting the searchers to the location of the organism. For monitoring to be more effective, we need to assess the probability of false negatives for different approaches and different species characteristics (e.g., mobility).

Creating and comparing the efficacy of alternative approaches for early detection has been recommended as an urgent area of research (Chinese Mitten Crab Working Group 2003). However, research on the topic is limited (Hayes et al. 2005). Capture–recapture approaches have shown promise to quantify an unbiased estimate of the probability of detection and false negatives (Otis et al. 1978, Pollock et al. 1990, MacKenzie et al. 2005). In this manuscript, we modify capture–recapture theory, integrating it with experimentally manipulated target and searcher densities in natural intertidal areas along the east coast of the USA, to test detection efficacy (i.e., the ability to detect at least one individual of a species in an area, if it exists). Further, we test different sampling approaches (quadrat vs. TAS) and different target characteristics (mobile vs. sessile). We produce a model to estimate the probability of detecting one individual in an area, given different target densities and search effort. Finally, we link these models to two years of survey data.

Study system

The focal organisms for this study (see Plate 1), the European green crab, *Carcinus maenas*, and the Asian shore crab, *Hemigrapsus sanguineus*, are both global invaders (Lohrer 2001, Breton et al. 2002, Carlton and Cohen 2003, Schubart 2003). These species are of great interest and importance to resource managers because both species not only can cause ecological damage, but also prey upon economically important species such as shellfish and other crabs (Elner 1981, McDonald et al. 2001, Walton et al. 2002, Griffen and Delaney 2007). The areas sampled were sites within the intertidal zone

of New England, New Jersey, and New York, which have already been invaded by *C. maenas* for almost 200 years and have been colonized by *H. sanguineus* in the last 25 years (Williams and McDermott 1990, Carlton and Cohen 2003, Kraemer et al. 2007). Furthermore, this region is at risk for invasions by other decapod species such as the Chinese mitten crab, *Eriocheir sinensis* (Herborg et al. 2007), which has colonized the central section of the east coast of the USA and has been detected as far north as New York. Because it can cause ecological and economical impacts (NYS DEC 2009), the IUCN has listed *E. sinensis* as one of the 100 worst invasive species (Lowe et al. 2000).

METHODS

Manipulative field experiment

In the summer of 2006 we conducted field experiments to determine the relationship between detection of at least one individual and the following factors: sampling intensity (i.e., number of searchers or time searching), target density, sampling technique (quadrat and total area search, TAS), and target mobility. The study was conducted across 40 sites from Rye, New York to Seal Harbor, Maine. Each site had from 1 to 49 people searching four 200-m² sections of the rocky intertidal zone, resulting in a sampling intensity ranging from 0.005 to 0.245 searchers/m². In total, 160 areas were searched for the experiment. Each search group used both the TAS and quadrat sampling for 10 minutes per 200-m² area. Participants randomly placed 1-m² quadrats and sampled as many as were possible during the time period. At each site, the order in which study areas were searched was randomized. We explicitly controlled for target density, by randomly placing different numbers of banded *H. sanguineus* and *C. maenas* crabs or oval marbles, to obtain a range of densities from 0.005 to 0.14 targets/m² (1–28 targets). At each site, one density level was used at all four 200-m² areas. Banding of crabs allowed us to distinguish targets from other crabs in the area, thereby controlling density. The crabs were banded with a single 6.35–25.4 mm metal ring on one of their chelipeds (i.e., claws), rather than on their walking legs, so as not to reduce their mobility. To minimize edge effects (crabs moving out of the search area), we created a buffer region around the study area in which we distributed the banded crabs at the intended density but over a larger total area (900 m²). To simulate sessile targets, we used flat oval marbles as a proxy, given the lack of sessile crabs. If the random coordinates where the marbles were to be allocated were locations where rocks occurred, the marbles were placed under that rock. These marbles, ranging from 12.7 to 25.4 mm, were in the middle of the size range for *H. sanguineus* and *C. maenas*; the average size (i.e., carapace width) for the 11 244 specimens of *H. sanguineus* and *C. maenas* collected during the 2006 survey was 19.7 ± 12.1 mm (mean ± SD). The marbles were randomly allocated to a 400-m² section of the rocky intertidal zone at each site,

which encompassed the two 200-m² study areas so that there was a study area to be searched by each of the two approaches, separately.

Statistical analysis

We tested whether sampling approach (quadrat vs. TAS) and mobility (crabs vs. marbles) affected detection by examining detection success (yes/no) as well as time to first detection (seconds) on a per site basis. We used 2×2 contingency tables with two-tailed chi-square tests with Yates' correction for continuity to determine whether mobility of target was a significant predictor of detection success (i.e., detectability) for either sampling approach, and to test whether there was a difference between the detection efficacy of the two sampling approaches. We used a block-design ANOVA for time to first detection, with site as a blocking variable and two fixed-effect within-block factors (mobility of target and the type of sampling approach). At one randomly selected site, Lovells Island, Boston, Massachusetts, USA, we recorded the sizes of all crabs collected by each sampling approach. Neither distribution was normally distributed (Kolmogorov-Smirnov test, $P < 0.010$), so the nonparametric Mann-Whitney test was used to determine if the TAS sampling approach collected individuals that were significantly different in size.

Detection model

We used multiple logistic regression to test for a relationship between probability of detection (POD) of at least one individual in an area, measured as the binary yes/no at each site, vs. sampling intensity and density of targets:

$$\text{POD} = \frac{e^{(a+bT+cS)}}{1 + e^{(a+bT+cS)}} \quad (1)$$

where T is the density of targets, S is the density of searchers, and a , b , and c are the regression coefficients. The complement of POD is the probability of a false negative. From the regression model we can calculate the sampling intensity needed to detect a certain target density with a given POD. To quantify the density of searchers and targets, we need to know the amount of area of intertidal zone for the region of interest (e.g., state, country). Unfortunately, the area or width of the intertidal zone is not always known, but the length of shoreline is known (Millhouser et al. 1998). From this, and by assuming that the average width of the intertidal zone is 30 m, we estimated the area of the intertidal zone for a region from its shoreline length (length of the shoreline multiplied by 30 m). This is an underestimate of the intertidal zone area, as it can almost reach a width of 1 km in certain areas of the Bay of Fundy. In 2005, all 52 sites within seven states (New Jersey to Maine) surveyed had an intertidal width greater than 30 m at low tide. Therefore this is a conservative estimate of the sampling intensity needed for monitoring.

Presence-absence surveys for *Hemigrapsus sanguineus*

To apply our detection model to a current environmental problem, we conducted systematic surveys using the TAS approach and randomly placed quadrats from May through August in 2005 and 2006. In 2005, 52 sites were sampled from Sandy Hook, New Jersey, to Machias, Maine, USA. A sampling site was defined as a 30×30 m section of rocky intertidal zone, which was suitable habitat for the introduced crab species *H. sanguineus* (Delaney et al. 2008). The sampling intensity varied from site to site, ranging from 1 to 69 people (0.001 to 0.077 searchers/m²). In 2006, 30 sites were sampled from Rye, New York to Lubec, Maine, with constant sampling intensity across the sites: 16 randomly placed 1-m² quadrats and 12 people, each searching 10 minutes within an area of 200 m² (0.06 searchers/m²), which was 10 vertical meters by 20 horizontal meters (Griffen and Delaney 2007).

RESULTS

Comparing sampling approaches and quantifying false negatives

Mobility of the target did not affect the detection success of the quadrat ($\chi^2 = 0.564$, $df = 1$, $P = 0.452$) or TAS approach ($\chi^2 = 0.779$, $df = 1$, $P = 0.377$). Therefore, detection success data for sessile and mobile targets were aggregated for each sampling approach. However, mobility of the target did increase the time to first detection ($F_{1,117} = 4.89$, $P = 0.029$). Sampling strategy was highly significant for both the continuous ($F_{1,117} = 108.41$, $P < 0.001$) and binary ($\chi^2 = 46.692$, $df = 1$, $P < 0.0001$) response variables in the corresponding statistical tests. TAS was a significantly better approach for detecting targets at lower densities of targets and searchers (Fig. 1). The searchers using the TAS approach detected the first target more quickly than with the random quadrat approach (Fig. 2). The TAS approach is more effective at detecting a species at lower target density, but is biased toward collecting larger individuals, on average, than the quadrat approach (Mann-Whitney test, $P < 0.001$). Of the crabs collected by the random quadrat approach, 29% were smaller than 1 cm, compared to only 10% of the crabs in this size class for the TAS approach. The large size class of >3 cm comprised 1.1% of the crabs collected by the quadrat approach, but comprised 7.7% of crabs collected by the TAS approach.

In a multiple logistic regression, the density of targets and sampling intensity were significant for both the quadrat and TAS approach (Table 1). For the TAS approach, the highest density of targets that was not detected was 0.07 targets/m², at a sampling intensity of 0.005 searchers/m² (i.e., a single searcher) and was half of the highest target density that the quadrat approach missed, 0.14 targets/m², which was also not detected at a site being monitored by a single searcher (Fig. 1).

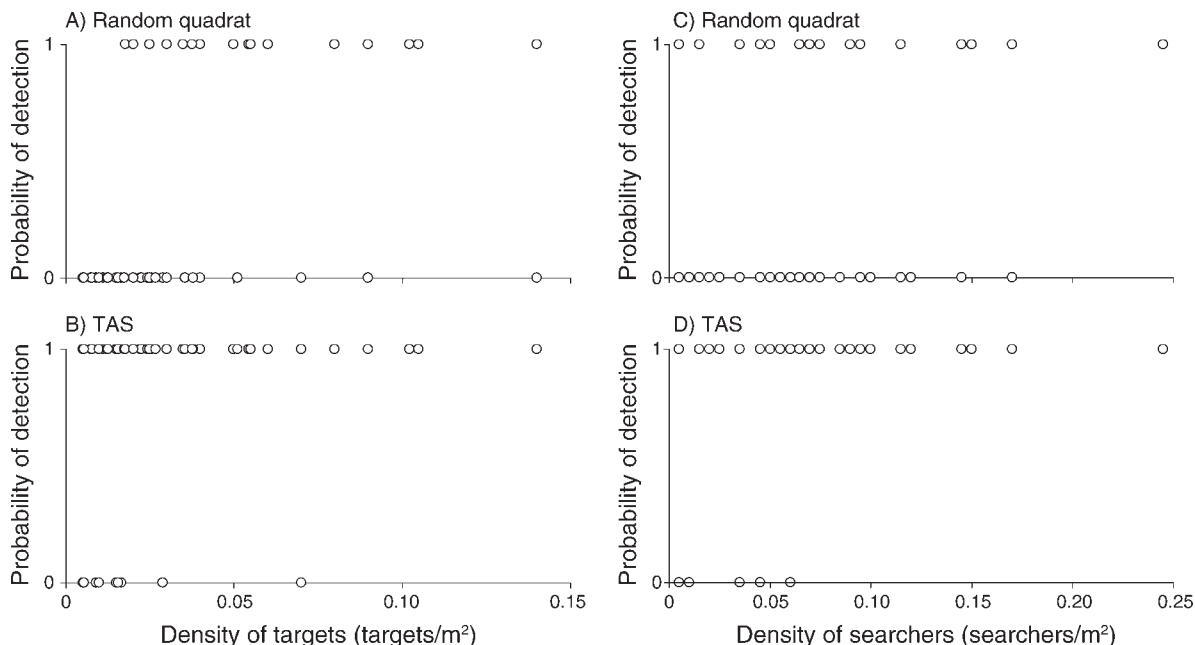


FIG. 1. (A, B) Probability of detection data (1 = detected, 0 = not detected) vs. density of targets for (A) random quadrat sampling and (B) TAS (total area search) sampling. (C, D) Probability of detection data vs. density of searchers for (C) random quadrat sampling and (D) TAS sampling. Because there was at least one target at each sampling area, all zeroes represent false negatives. Results are combined for both types of targets: mobile (banded crabs) and sessile (marbles).

Detection model

The multiple logistic regressions generated the needed coefficients (Table 1) to parameterize the statistical model based on Eq. 1. The model coefficients were used

to calculate contour plots of the probability of detection as a function of the density of searchers and targets (Fig. 3). This model applies when the sampling intensity and density of the targets are both greater than zero. Using

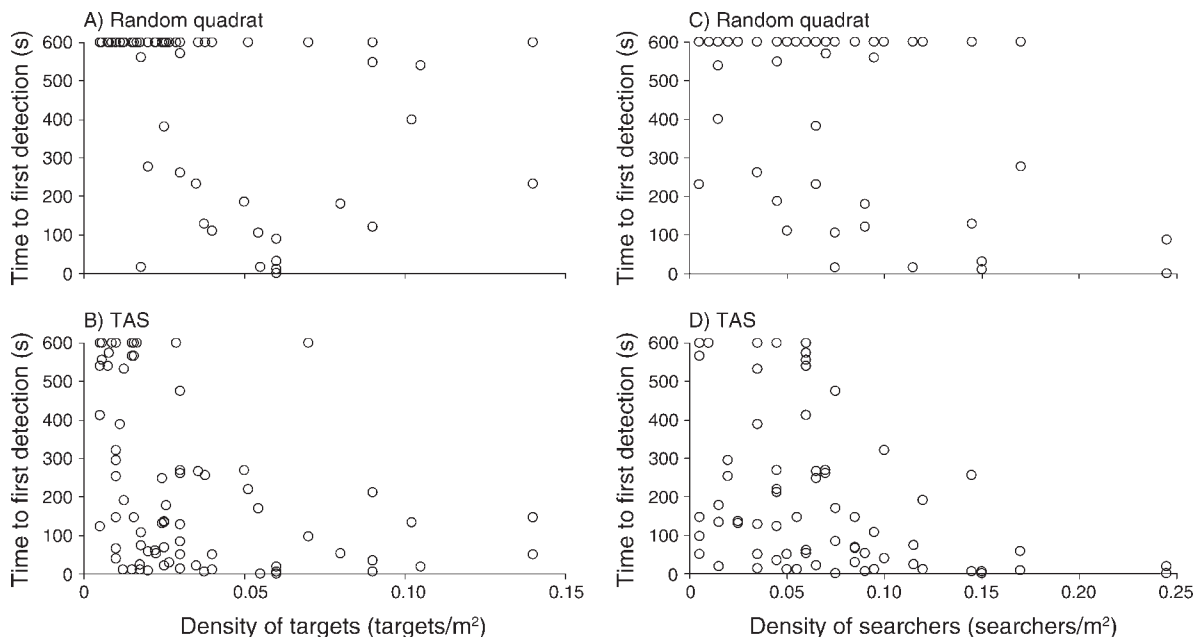


FIG. 2. (A, B) Time to first detection (in seconds) vs. density of targets for (A) random quadrat sampling and (B) TAS sampling. (C, D) Time to first detection vs. density of searchers for (C) random quadrat sampling and (D) TAS sampling. The maximum search time is 10 minutes, so data points at 600 s are false negatives.

TABLE 1. Multiple logistic regression was used to create probability of detection (POD) curves for both the quadrat and total area search (TAS) sampling approaches for mobile (banded crabs) and sessile targets (marbles).

Sampling approach and parameter	Symbol	Coefficient	SE	Z	P
Total area search, TAS					
Constant	<i>a</i>	-1.988	0.791	-2.51	0.012
Target density	<i>b</i>	45.340	23.032	1.97	0.049
Sampling intensity	<i>c</i>	72.723	20.989	3.46	0.001
Quadrat search					
Constant	<i>a</i>	-4.512	0.948	-4.76	<0.001
Target density	<i>b</i>	48.380	12.214	3.96	<0.001
Sampling intensity	<i>c</i>	25.297	8.178	3.09	0.002

Note: The regression coefficients used in Eq. 1 are displayed with standard error, Z score, and P value for the two sampling approaches.

an estimated intertidal width of 30 m, the model was used to calculate the amount of time needed to monitor the coast of a certain area, such as a site, an entire state, or a country. To realize a 95% POD of at least one invader present in a 200-m² section of intertidal zone would require a total of 2.2 h of TAS sampling; for the quadrat sampling approach, 9.5 h of total searching would be required. To monitor New Hampshire, the state with the smallest coastline in our study area (211 km), would require a minimum of ~301 000 h of quadrat sampling to have a 95% POD of an invader at a low density of 0.005 crabs/m². The TAS approach

would require 68 300 hours of sampling along the coast of New Hampshire. On a national scale, to have this level of effectiveness, using the quadrat approach, would require at least 203 000 000 hours of sampling; with the TAS approach it would require 46 200 000 h of sampling. Other states in the study area were somewhere in this range for sampling intensity needed (Fig. 4). Given these conditions, the TAS approach requires less than one-fourth of the sampling intensity than does the random quadrat approach to achieve the same level of effectiveness. Both, however, require an exorbitant amount of effort.

Presence-absence surveys for *Hemigrapsus sanguineus*

In 2005, 1–69 people conducted the random quadrat sampling technique and the TAS approach, so the POD varied from site to site due to different sampling intensities. If one crab was present at a site, a single person carrying out a search would have a POD of 1.2%

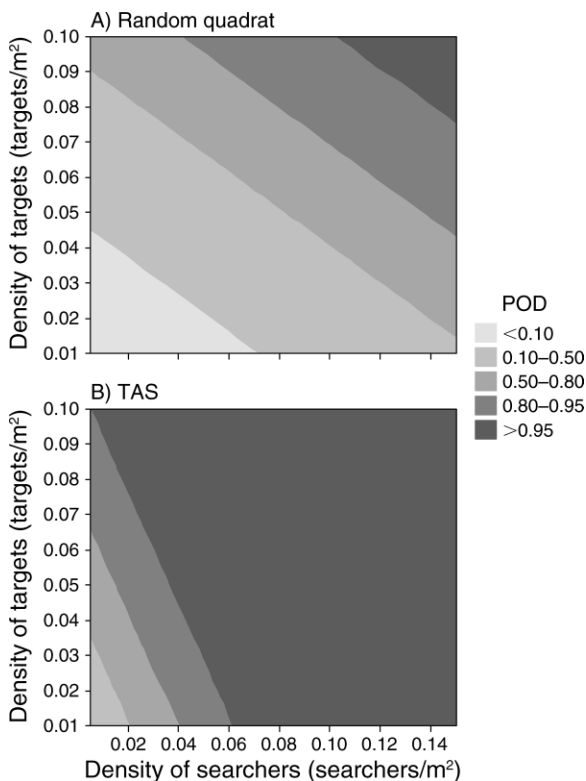


FIG. 3. Contour plots of predicted probability of detection (POD) vs. density of searchers and density of targets for (A) the random quadrat and (B) the TAS approach.

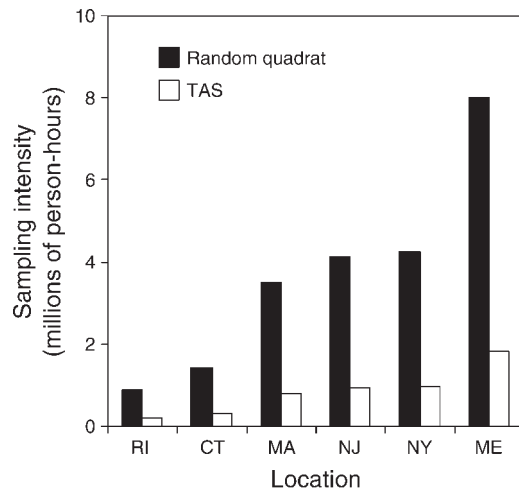


FIG. 4. Estimated minimum number of person-hours needed to detect an invader at a density of 0.005 crabs/m² with a 95% probability of detection for the TAS approach (open bars) and the random quadrat approach (solid bars) for the coasts of Connecticut (CT), Maine (ME), Massachusetts (MA), New Jersey (NJ), New York (NY), and Rhode Island (RI), USA.

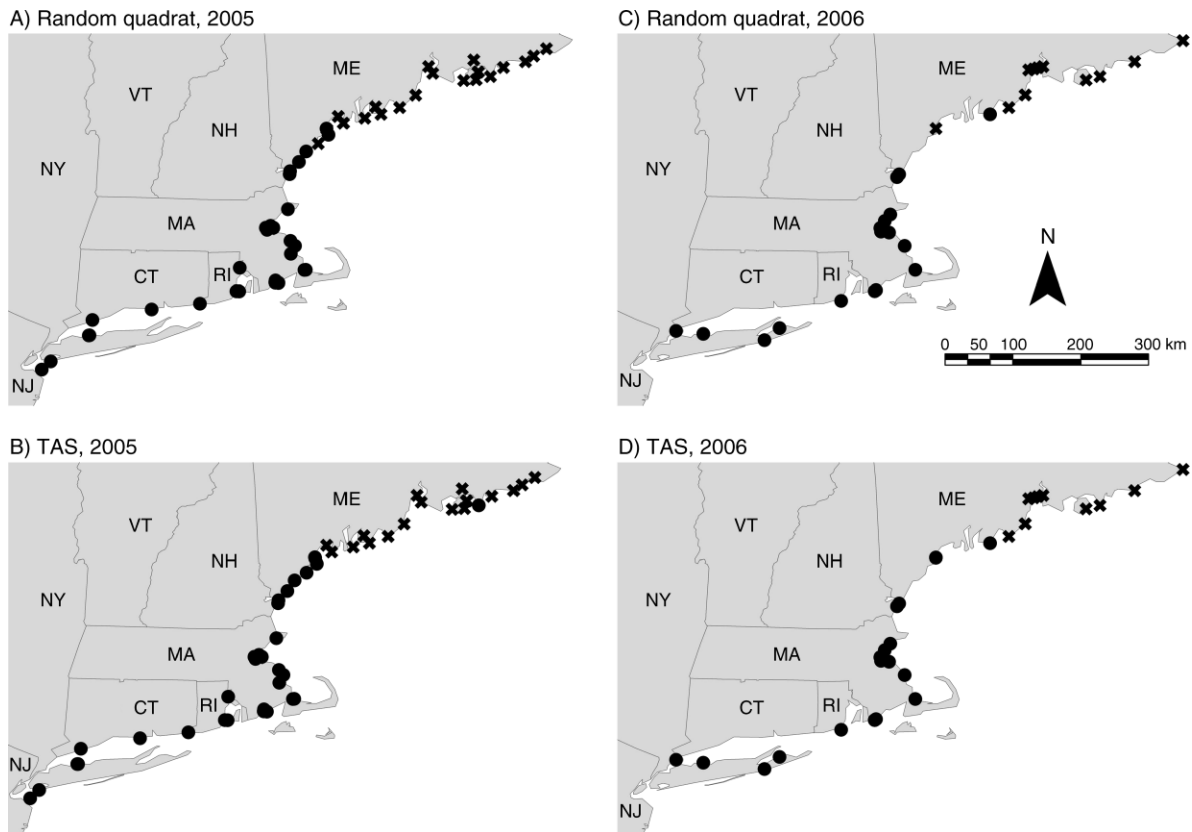


FIG. 5. The 2005 survey, including (A) random quadrat sampling and (B) TAS sampling, consisted of 52 sites from Sandy Hook, New Jersey (NJ), to Machias, Maine (ME). The sampling intensity varied across sites. The 2006 survey including (C) random quadrat sampling and (D) TAS sampling was conducted with even sampling intensity at 30 sites from Rye, New York (NY), to Lubec, Maine. Solid circles denote locations where *Hemigrapsus sanguineus* was detected; heavy "x" symbols denote sites that were sampled, but where *H. sanguineus* was not detected.

and 13.5% for the quadrat and TAS approach, respectively. For 69 people searching a site with the same target density, the POD would be 7.4% and 97.4% for the quadrat and TAS approaches, respectively. Both the TAS and quadrat surveys conducted in 2005 showed a discontinuous distribution of *H. sanguineus* (Fig. 5A, B). The 2006 quadrat survey (Fig. 5C) found a discontinuous distribution, whereas the 2006 TAS survey (Fig. 5D) documented a continuous distribution. In the 2006 quadrat survey, given a constant sampling intensity across sites, there was a 6.0% POD whereas the TAS approach had a 93.1% POD.

DISCUSSION

Detection

Detection is a critical component of management strategies, maximizing the ability to respond rapidly and most effectively to novel invaders (Lodge et al. 2006). Further, it is highly relevant for interpretation of survey results, which often rely on presence-absence data (e.g., National Parks Service's All Taxa Biodiversity Inventory). Presence-absence data are becoming more popular, given new statistical approaches to use the data

and as it is readily available, cheaper, and easier to obtain on a large scale (Pereira and Itami 1991, Hanski 1994, MacKenzie et al. 2002, 2003, Tyre et al. 2003, Wintle et al. 2005). Although widely acknowledged, it is difficult to quantify the uncertainty in detection by a sampling approach. Therefore, many researchers and managers assume that the rate of false negatives is negligible for presence-absence survey data, even though they have been recorded to be as high as 87% (Wintle et al. 2005). In this study, we found that the probability of a false negative in survey data can be even higher (94% for quadrat sampling). Therefore, researchers examine their data, creating and analyzing patterns that might be inherently flawed. However, if identifying and quantifying uncertainty were possible, researchers and managers would be able to incorporate it into models or at least quantitatively assess the reliability of data. For monitoring, it can determine the feasibility of a certain survey or monitoring objective.

Quantifying the probability of detection

Given the importance of quantifying false negatives, researchers have developed different methodologies to



PLATE 1. (Upper) Dorsal view of the Asian shore crab (*Hemigrapsus sanguineus*), and (lower) the European green crab (*Carcinus maenas*). Photo credits: D. G. Delaney.

assess and ameliorate these issues (MacKenzie et al. 2005). Our experimental approach yields an unbiased estimate of the probability of detection, because we know that one or more targets are present at each site; hence every non-detection is a false negative and is quantified. This type of experimental approach can quantify the actual probability of detection and false negatives and can help us to better understand and interpret presence-absence survey data and design better monitoring programs.

The probability of detection is strongly affected by the density of searchers and targets, but many other factors could also negatively or positively affect the probability of detection. These factors include, but are not limited to, the size, behaviors, and color of the organism and external factors (e.g., habitat, weather). What factors increase or decrease the probability of detection could have management implications. For example, the probability of detection may be lower for small and young individuals. Nevertheless, if we can detect the invader before sexual maturity, eradication theoretically may still be possible (Edwards and Leung 2009).

The methods and experiment developed in this paper would allow researchers to determine if these and other factors for species detection are important, and to quantify an unbiased estimate of the probability of detection, which would allow for better management of a species. Particularly, the approaches presented in this manuscript are most applicable for sessile (e.g., algae, barnacles, bryozoans, hydroids, tunicates, and so forth) and slow-moving organisms (e.g., clams, chitons, other species of crabs, limpets, nudibranchs, sea urchins, sea stars, snails, and so forth), which will remain in the study area, permitting estimation of their densities. Such slow-moving or sessile organisms are common invasive species and are highly abundant in the intertidal zone. Therefore, this experimental approach will be relevant for a large subset of invasive species.

A case study: monitoring invasive species in Salem Sound

Refining sampling approaches can increase the abilities of monitoring groups to detect newly arriving invasive species. Salem Sound is a large, well-studied embayment north of Boston, Massachusetts, with an intertidal zone area of ~ 4.8 million m^2 (1186.58 acres) (Chase et al. 2002). To date, the intertidal zone of Salem Sound has been documented to contain at least 12 introduced species, including *C. maenas* and *H. sanguineus*. This area is at risk for future invasions by other decapod crustaceans such as *E. sinensis* and the brush-clawed shore crab *Hemigrapsus takanoi*, and it is currently monitored by a nongovernmental organization (NGO) called Salem Sound Coastwatch. This organization, like most NGOs is small, having only 1–3 paid staff at any time, so they train volunteers to monitor the coastline for introduced species in Salem Sound. In 2005 and 2006, Salem Sound Coastwatch trained 30 volunteers to monitor Salem Sound (B. Warren, *personal communication*). The methodology was used to conduct monthly monitoring in the summer, using randomly placed quadrats in the high- and the low-intertidal zone to detect introduced species that were present in Salem Sound.

Using the model developed in this paper, we can quantify the probability of detecting an invader at any density, given its sampling intensity, for the area of intertidal zone of Salem Sound using their current sampling approach, and compare it to their effectiveness of using the TAS approach. We estimate that with a sampling intensity of 30 people, each searching 10 minutes, there is a 1.4% or 14.7% probability of detecting an introduced species at a density of 0.005 crabs/ m^2 in the intertidal zone of Salem Sound using the random quadrat sampling or TAS approach, respectively. The TAS approach is an order of magnitude more effective in its ability to detect species at low densities than is the quadrat approach. Unfortunately, even with the better sampling approach, early detection is still a low-probability, labor-intensive task. To have a 95% probability of detecting an invader in Salem Sound at a

density of 0.005 crabs/m² would require 26 or 115 full-time personnel (i.e., 2000 h/person) monitoring with the TAS and quadrat approach, respectively. In 2007 the personnel and volunteers of Salem Sound Coastwatch switched from mainly using the random quadrat sampling approach, which they had used for the previous three years, to primarily using the TAS approach, based on our recommendation (B. Warren, *personal communication*).

Comparing alternative sampling approaches

We recommend quantitative experiments to determine the abilities and limitations of a sampling approach, because every sampling technique has different strengths and weaknesses. We offer a search theory approach that will help scientists and practitioners to quantitatively compare alternative sampling approaches in a standardized manner. Although random quadrat sampling is the most common way to sample an area (Chiarucci et al. 2003) because it can enumerate estimates of population structure (Wernberg 2009) and abundance (Rueda and Salas 2008), it is not effective at detecting organisms at low densities (Figs. 1 and 2). The TAS approach is more effective at detecting organisms low in abundance; the trade-off is that TAS is biased toward finding larger individuals. Also the TAS approach is currently not able to quantify the density of a species, but this may be possible and should be an area for future research. However, the TAS approach is a more powerful and simpler technique than random quadrat sampling. It is more easily performed by volunteers, which increases sampling intensity, as seen in Salem Sound. This type of program should be done in other regions because the entire east coast of North America is at risk for the establishment of *E. sinensis* (Herborg et al. 2007). We have demonstrated that these sampling approaches have significantly different abilities to detect the focal organisms, and this can have important ramifications. For this reason, we need to better understand what the best sampling approach is for a given objective. The type of experimental approach in this study can be used to compare other sampling techniques (e.g., trapping). For early detection to be possible, we need new sampling approaches and experiments to evaluate their efficacy and sensitivity for monitoring various species at low densities.

Avoidance

The probability of detecting a species at low densities, which has been shown to increase the probability of successful eradication, could be species specific (Hayes et al. 2005). The optimal sampling approach may be determined by the biological characteristics of the focal species, such as mobility. Certain sampling approaches, such as quadrat or transect sampling, take initial setup before sampling occurs that could allow motile organisms to move out of the sampling area and therefore not be detected (Hayes et al. 2005). This has been called

avoidance and could be an important factor affecting the detection of motile organisms (Bohnsack 1979). We found that motile organisms took longer to detect than our proxy for sessile organisms, which is evidence of the existence of avoidance, but did not significantly affect detection success. We hypothesize that this is the case for the focal species of this study because when startled they usually hide under the closest rock. In other environments or for other species, the disturbance of placing a quadrat or laying out a transect could result in the organisms leaving the search area and could increase the importance of avoidance in the form of reduced detection success (Hayes et al. 2005). Therefore, avoidance should be studied further with different species, as it may hinder our ability to rapidly and effectively detect species at low densities, which is critical for successful control and eradication programs.

To date there have only been a handful of successful eradications of marine introduced species and early detection was key (Bax et al. 2001, Kuris 2003). Our review of the relevant peer-reviewed literature found that all of the marine introduced species that have been successfully eradicated are organisms with completely sessile adult life stages. The only possible exception is the eradication of a tube-dwelling sabellid polychaete *Terebrasabella heterouncinata* from Cayucos, California by removing adult snails, which act as host species for the invader (Culver and Kuris 2000, Kuris 2003). An example of a sessile adult organism being successfully eradicated is the black-striped mussel *Mytilopsis sallei* (Kuris 2003). It was detected in Darwin, Australia, possibly within the first six months after it was introduced (Bax 1999, Kuris 2003); nine days after it was detected, a rapid response plan was agreed upon and initiated, which resulted in successfully eradicating *M. sallei* (Bax et al. 2002). Understanding how biological characteristics affect detectability will help in selecting a sampling approach to detect a target species or at least identify what species might be easier to detect and eradicate, and guide funding and policy decisions.

Detectability in presence-absence surveys

Non-detection does not necessarily mean nonoccurrence of a species. The 2006 quadrat survey displays a discontinuous distribution of *H. sanguineus* because the organism was not detected at one site within its known distribution. The probability that our 2006 quadrat survey missed detecting *H. sanguineus*, if present, at this site could be as high as 94%. Therefore, there is a high probability of a false negative being recorded at this site. This is confirmed by the fact that the TAS approach detected *H. sanguineus* at this site on the same day that it was not detected by the quadrat approach (Fig. 5C, D). The 2006 TAS survey data set (Fig. 5D) depicts a continuous distribution of *H. sanguineus* with a boundary of its distribution in Maine, but how confident are we in this conclusion? This question is similar to

observing an apparent gap in the surveyed distribution of a species. The probability of the conclusion being correct (PCC) decreases with the probability of not detecting (POND) a species and increases with the number of repeated surveys (N) in a gap or boundary region with no detections:

$$\text{PCC} = 1 - \text{POND}^N. \quad (2)$$

In this case we surveyed 10 sites in northern Maine and did not detect the presence of *H. sanguineus* at any of these sites. The POND for a single invader, if present, was 6.9%. Therefore the probability of this actually being a boundary is $\gg 99.9\%$. This is supported by the fact that, to date, *H. sanguineus* has not been detected along the coast of Canada.

Solution to a personnel problem

Limited sampling intensity can lead to false negatives and survey data with misleading depictions of species distributions (e.g., Fig. 5C). Accurately recording this type of data and early detection of newly arriving invasive species require high levels of sampling intensity. To illustrate this point, we have considered the minimal amount of personnel or time that would be needed to monitor the coastline in its entirety with equal level of sampling intensity (Fig. 4). Even with TAS, the more efficient sampling approach, 23 100 people working full time would be needed to monitor the coast of the USA. This is too labor-intensive to be feasible and more effective and practical strategies must be found.

To overcome this challenge we recommend a multi-pronged approach of prevention, increased funding for monitoring, creating a predictive spread model to prioritize areas to monitor, and incorporating trained volunteers in monitoring. Prevention can be more cost effective than managing the impacts of an invader (Leung et al. 2002, Bax et al. 2003). Unfortunately, no matter how effective prevention programs are, they will never be 100% effective and species will still be colonizing, so we must continue to monitor, especially in certain areas of the coast that are more likely to be colonized (e.g., seaports, most suitable habitats of the invader) (Lodge et al. 2006). Advances in theoretic understanding are occurring in invasion biology, that predict habitat suitability and dispersal patterns for a species (e.g., Leung and Mandrak 2007). These advances allow us to identify areas at highest risk and would provide a way to ameliorate the personnel limitations for large-scale monitoring. The most cost-effective option is incorporating citizen scientists (i.e., trained volunteers) in monitoring. Scientists can easily recruit volunteers in large numbers and, with the aid of a field guide, volunteers can identify native and invasive species of crabs with high levels of accuracy (Delaney et al. 2008). Citizen scientists can increase the sampling intensity in areas that are currently being monitored and can monitor areas that are not currently being monitored. Also the TAS approach, which is more

effective for detecting species at low densities, is simpler and easier for volunteers to execute. Even with the most effective approach and incorporating volunteers in monitoring, we may not have sufficient personnel to monitor the entire coast with the level of intensity that is needed for early detection. We probably still need to further reduce the amount of labor by continued experimentation on other sampling approaches (e.g., trapping) to optimally monitor.

This problem of limited resources and vast amounts of area to monitor is a common and challenging problem for practitioners and ecologists, but the solution may come from a different field that has had to deal with a similar problem: optimal allocation of search effort (Koopman 1953, Stone 1989). During World War II, search theory was developed by Bernard Koopman and the Anti-Submarine Warfare Operations Research Group of the U.S. Navy to optimally detect German submarines in the Atlantic Ocean with limited resources (Koopman 1946, 1980). The goal was to determine the best way to detect enemy submarines and to maximize the chance of success by using different search patterns, while minimizing the amount of equipment and personnel needed. Later, search theory helped the U.S. Coast Guard to guide search and rescue missions, doubling or tripling successful rescues (Cooper et al. 2003). Although this area of research has been used mainly by the military, recently it has been suggested to have useful applications in the field of ecology (Cacho et al. 2007). However, it has not yet been used in ecological surveys in marine systems. We propose that search theory could inform ecologists and resource managers how to optimally allocate limited resources, such as personnel, and determine what is the best approach for a certain survey or monitoring objective.

In summary, because labor is limited, our ability for early detection is greatly hampered and this leads to many false negatives in large-scale presence-absence survey data. Predictive spread models would identify areas of high risk for colonization, so if we cannot monitor everywhere, given the same sampling intensity, we maximize our chance for detection by searching high-risk areas. We recommend involving citizen scientists and conducting quantitative search theory experiments to determine optimal sampling techniques and areas to search. Our experimental approach used in this study allows quantitative comparison of sensitivity and efficacy of different approaches and quantifies the probability of detection. We created a model that dynamically calculates sampling intensity needed depending on different levels of effectiveness and spatial scales (a site, region, state, or country). The problems, as well as the approaches, are generalizable. By quantifying the limitations of sampling approaches and data, researchers and managers can better understand patterns in presence-absence survey data, which allows for better research, management, and policy decisions.

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