



Differential escape from parasites by two competing introduced crabs

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ABSTRACT: Although introduced species often interact with one another in their novel communities, the role of parasites in these interactions remains less clear. We examined parasite richness and prevalence in 2 shorecrab species with different invasion histories and residency times in an introduced region where their distributions overlap broadly. On the northeastern coast of the USA, the Asian shorecrab *Hemigrapsus sanguineus* was discovered 20 yr ago, while the European green crab *Carcinus maenas* has been established for over 200 yr. We used literature and field surveys to evaluate parasitism in both crabs in their native and introduced ranges. We found only 1 parasite species infecting *H. sanguineus* on the US East Coast compared to 6 species in its native range, while *C. maenas* was host to 3 parasite species on the East Coast compared to 10 in its native range. The prevalence of parasite infection was also lower for both crabs in the introduced range compared to their native ranges; however, the difference was almost twice as much for *H. sanguineus* as for *C. maenas*. There are several explanations that could contribute to *C. maenas*' greater parasite diversity than that of *H. sanguineus* on the US East Coast, including differences in susceptibility, time since introduction, manner of introduction (vector), distance from native range, taxonomic isolation, and the potential for parasite identification bias. Our study underscores not just that non-native species lose parasites upon introduction, but that they may do so differentially, with ramifications for their direct interactions and with potential community-level influences.

KEY WORDS: *Carcinus maenas* · *Hemigrapsus sanguineus* · Introduced species · Parasite richness · Parasite prevalence

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INTRODUCTION

Throughout seafaring history, ships traveling from port to port have facilitated the introduction of species to foreign habitats (e.g. Carlton & Geller 1993). Successful invaders often benefit from a lack of, or a reduction in, many of the ecological and/or physical constraints which restrict the invader's density, range, and ecological niche in its native territory (e.g. Min-

chella & Scott 1991, Cohen & Carlton 1998, Ruiz et al. 2000, Torchin et al. 2005), often resulting in enhanced fitness in the new habitat (e.g. Torchin et al. 2003, Sax et al. 2007). In particular, invading species often leave behind predators and parasites in their native regions (Torchin & Mitchell 2004).

While several studies have compared parasitism of a single species in native versus introduced range(s) (see review in Torchin & Mitchell 2004), fewer have

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evaluated multiple introduced species within a single region and how escape from enemies such as parasites could influence interactions between or among species that inhabit similar niches (Settle & Wilson 1990). A notable single species example of parasite escape is the European green crab *Carcinus maenas*. Since its appearance on the North American East Coast ~200 yr ago (Carlton & Cohen 2003), the crab has spread from Virginia, USA, to Atlantic Canada (Delaney et al. 2008), and it has had both ecologically and economically significant impacts on the native biota of its introduced range (Glude 1955, Ropes 1968, Lohrer & Whitlatch 2002). In its native Europe, parasitism (specifically by parasitic castrators) is common and negatively correlated with the average body size and biomass of crab populations, while in North America, crabs are unparasitized by castrators, are larger, and are more abundant than in Europe, suggesting a fitness benefit from reduced parasitism (Torchin et al. 2001).

A more recent invader to the northeastern USA, *Hemigrapsus sanguineus* (Asian shorecrab), is now vying with *Carcinus maenas* as the most abundant US East Coast shorecrab. *H. sanguineus* was first observed in Long Island Sound, USA, in 1988 (McDermott 1998) and has since increased its range southwards to North Carolina and northwards into southern Maine (Delaney et al. 2008), monopolizing the majority of rocky intertidal habitats within this region (Kraemer et al. 2007). In much of its new range, *H. sanguineus* has displaced *C. maenas* as the most abundant rocky intertidal crab (Ahl & Moss 1999, Lohrer & Whitlatch 2002, Griffen & Byers 2009), occurring at twice the average density (and up to 10 times the density) of *C. maenas* in the intertidal zone (Griffen & Byers 2009). While *H. sanguineus* and *C. maenas* co-occur in the Gulf of Maine, the southern densities of *C. maenas* have declined precipitously due, at least in part, to strong negative interspecific interactions between the crabs (Tyrrell & Harris 1999, Lohrer & Whitlatch 2002, Griffen et al. 2008, Griffen & Byers 2009). On the whole, the introduction of *H. sanguineus* has resulted in a substantial shift in the most common New England intertidal shorecrab over the last couple of decades (e.g. Jensen et al. 2002, Lohrer & Whitlatch 2002, Tyrrell et al. 2006, Kraemer et al. 2007, Griffen et al. 2008, Griffen & Byers 2009).

While parasites of *Carcinus maenas* in native and introduced populations have been evaluated in detail (Torchin et al. 2001, Kuris et al. 2005), parasites of *Hemigrapsus sanguineus* in its newly invaded North American range have yet to be adequately quantified. We therefore sought to quantify parasitism of *H. sanguineus* where it overlaps with *C. maenas* on the US East Coast and also within its native Asian range

using successful techniques employed for *C. maenas* (Torchin et al. 2001, J.E.B. unpubl.). We then compared these results to a combination of published, unpublished, and new parasite data for *C. maenas* in its introduced and native ranges.

MATERIALS AND METHODS

To obtain parasite richness and prevalence data for *Carcinus maenas* (Brachyura: Portunoidea: Portunidae), we used the following records: (1) field and literature data from Torchin et al. (2001) and Kuris et al. (2005) for Europe and the US East Coast; (2) previously unpublished European field data (sites in Spain, Portugal, France, Great Britain, Norway, Sweden, and Netherlands) collected by M.E.T., A.M.K., and K.D.L. in 2000; and (3) 2 new East Coast field sites (Appledore Island, Maine and Adams Point, New Hampshire) collected in 2007 (Table 1). Parasites were identified by A.M.H.B. and C.L.K. and confirmed by A.M.K. and/or M.E.T. Sites used in analyses were chosen over a broad geographic scale to encompass a large proportion of the crab's range on both Atlantic coasts (Fig. 1, Table 2) and included both estuarine and coastal locations. Adult crabs were hand-collected in the intertidal zone with baited traps.

For *Hemigrapsus sanguineus* (Brachyura: Grapsoidea: Varunidae), native parasite diversity has been only partially documented in the literature (Torchin et al. 2001, McDermott 2007), and nothing has yet been compiled to show overall parasite richness in the crab in either the native or introduced populations. In its native Asian range, some information on individual parasites has been compiled (e.g. Otagaki 1958, Bridgman 1971, Yamaguchi et al. 1984, Takahashi & Matsuura 1994, Kifune & Koga 1999; see Table 1). We used these literature records as well as previously unpublished field data collected by A.M.K. and K.D.L. in 1995 from Japan to establish parasite species richness and prevalence in native *H. sanguineus* populations. For this latter work, *H. sanguineus* crabs were collected from 7 sites throughout much of Japan (Fig. 1, Table 2). In its introduced US East Coast range, little is known about parasite diversity of *H. sanguineus*, with the exception of 2 studies: Torchin et al. (2001) in Ocean City, MD, where 27 crabs were investigated and 1 larval nematode was found, and McDermott (2007) in Cape May, NJ, where 250 crabs were investigated and no parasites were found. Therefore, in the summer and fall of 2007 we collected and dissected an average of 20 crabs site⁻¹ from 7 geographically spaced sites (Fig. 1, Table 2). Crabs used in analyses were all adults and were hand-collected in the intertidal zone from coastal sites.

Table 1. Total parasite species richness in *Carcinus maenas* and *Hemigrapsus sanguineus* in native and introduced regions. Data include literature and field records from sources indicated in the citation column

Parasite	Type of parasite	Locations	Source
<i>Carcinus maenas</i>			
Native			
<i>Profillicollis botulus</i>	Acanthocephalan	Scotland	Thompson (1985), Torchin et al. (2001) [as <i>Polymorphus</i> sp.]
Trypanorhynch cestode	Cestode	Spain	Kuris et al. (2005), Torchin et al. (2001)
Tetraphyllid cestode	Cestode	Spain, Portugal	Kuris et al. (2005), M.E.T., A.M.K., K.D.L. (unpubl.)
<i>Portunion maenadis</i>	Isopod	England, Denmark, France, Portugal, Sweden	Bourdon (1960, 1963, 1964), Crothers (1968), Rasmussen (1973), Torchin et al. (2001)
<i>Thelohania maenadis</i>	Microsporan	Spain	Kuris et al. (2005), M.E.T., A.M.K., K.D.L. (unpubl.)
<i>Abelspora portulacensis</i>	Microsporan	Spain	Kuris et al. (2005), M.E.T., A.M.K., K.D.L. (unpubl.)
<i>Carcinonemertes carcinophila</i>	Nemertean	Netherlands, Belgium, England, France, Scotland	Humes (1942), Crothers (1968), Comely & Ansell (1989), Torchin et al. (2001) (as <i>Carcinonemertes</i> sp.)
<i>Sacculina carcini</i>	Rhizocephalan	England, Scotland, Wales, Ireland, France, Spain, Sweden, Denmark	Bourdon (1960, 1963), Crothers (1968), Rasmussen (1973), Minchin (1997), Mathieson et al. (1998), Torchin et al. (2001)
<i>Microphallus similis</i>	Trematode	England, Wales, France, Netherlands, Norway, Portugal, Spain, Sweden	Crothers (1968), Torchin et al. (2001)
<i>Microphallus primas</i>	Trematode	Portugal	Castilho & Barandela (1990)
Introduced			
<i>Profillicollis botulus</i>	Acanthocephalan	Eastern Canada, Maine, New Hampshire, Massachusetts	Bratley et al. (1985), Torchin et al. (2001) (as <i>Polymorphus</i> sp.), present study
Unidentified larval nematode ^a	Nematode	Maine, New Hampshire, Maryland	Torchin et al. (2001), present study
<i>Microphallus similis</i>	Trematode	Eastern Canada, Maine, New Hampshire, Massachusetts, Rhode Island, Connecticut	Stunkard (1956), Bratley et al. (1985), Torchin et al. (2001), present study
<i>Hemigrapsus sanguineus</i>			
Native			
Unidentified microsporan	Microsporan	Japan	Present study
<i>Polyascus</i> (= <i>Sacculina</i>) <i>polygenea</i>	Rhizocephalan	Japan, Russia	Yamaguchi et al. (1984), Korn et al. (2000, 2004), Isaeva et al. (2001, 2005), present study
<i>Sacculina senta</i>	Rhizocephalan	Japan	Takahashi & Matsuura (1994), Lützen & Takahashi (1997)
<i>Maritrema setoensis</i>	Trematode	Japan	Bridgman (1971), present study
<i>Microphalloides japonicus</i>	Trematode	Japan	Kifune & Koga (1999), present study
<i>Macrophallus</i> (= <i>Probolocoryphe</i>) <i>asadai</i>	Trematode	Japan	Otagaki (1958), present study
Introduced			
Unidentified larval nematode ^a	Nematode	Connecticut, New York, Delaware, Maryland	Torchin et al. (2001), present study
^a Parasites found in the introduced range but not found in the native ranges			

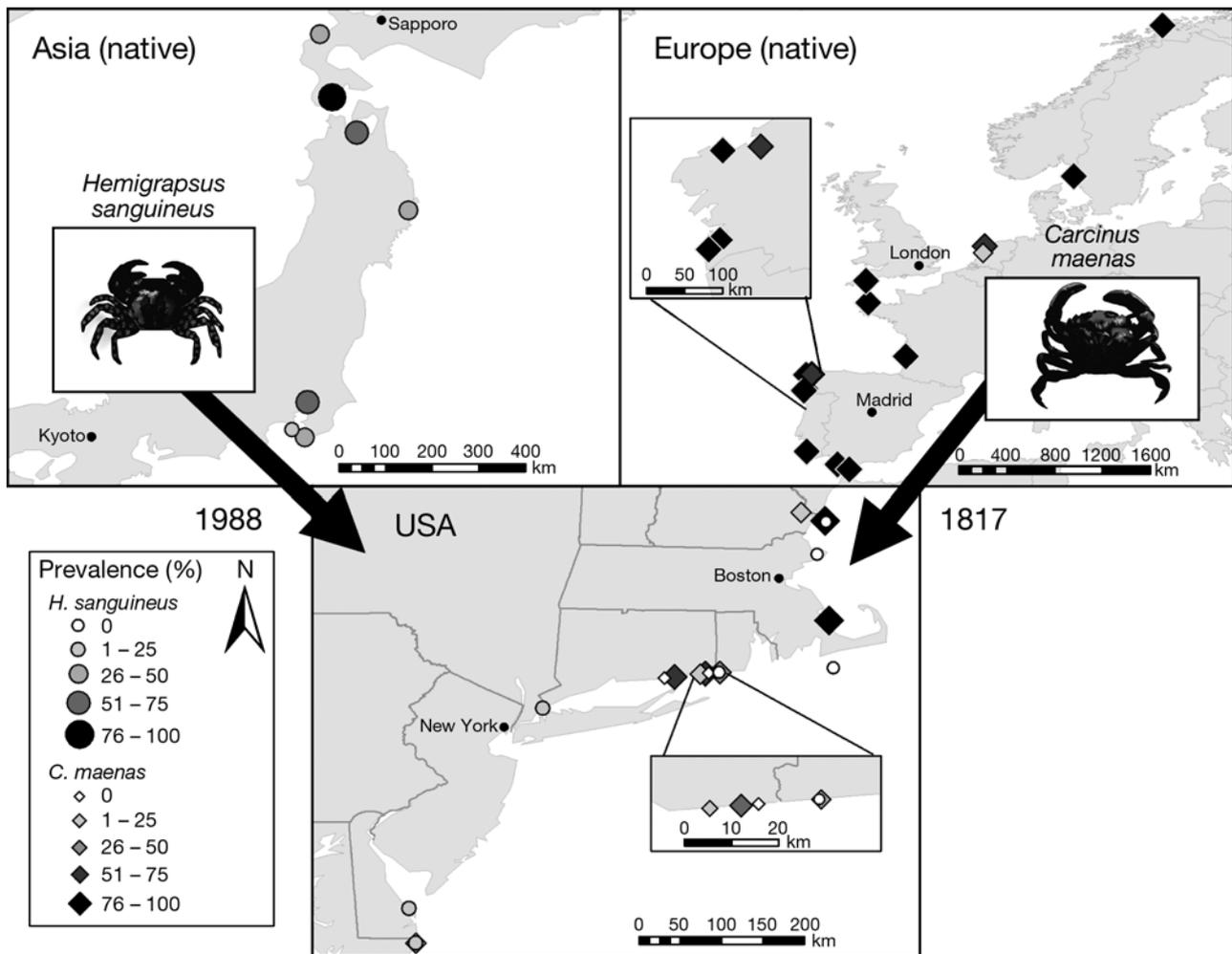


Fig. 1. *Hemigrapsus sanguineus* and *Carcinus maenas*. Maps, prevalence, and invasion history information. Circles represent sample sites for *H. sanguineus* in its native Asian and introduced US East Coast populations; diamonds represent sample sites for *C. maenas* in its native European and introduced US East Coast populations. Circles and diamonds are relatively sized and colored on a gradient of white to black depending on parasite infection prevalence (%) at each sample site. Dates are the accepted years of introduction for both crab species to the US East Coast

Our dissection protocol for both crab species was based on protocols by Torchin et al. (2001) and J.E.B. (unpubl.), which consisted of removing the crab's carapace and first visually inspecting all tissues under a dissecting microscope. We then systematically examined tissues from the crab's digestive cecum, body cavity, reproductive tissues, and thoracic ganglia under a compound microscope for the presence of metazoan parasites (e.g. acanthocephalans, cestodes, nematodes, trematodes). All crabs examined were fresh (not preserved) when dissected.

To quantify a host's escape from parasites, we calculated the proportional parasite escape for each crab species, which is: $(N - I)/N$, where N = the total parasite species richness of the native region and I = total para-

site species richness of the introduced region (Torchin et al. 2003). For both *Carcinus maenas* and *Hemigrapsus sanguineus*, our total species richness and parasite escape calculations included a combination of field and literature data. For all other richness and prevalence analyses, we used our field data only (i.e. we did not include literature records) to be consistent with the Torchin et al. (2001) and previously unpublished field data (M.E.T., A.M.K., K.D.L.), which explored particular parasite taxa (acanthocephalans, cestodes, epicaridean isopods, microsporans, nematodes, nemertean, rhizocephalans, and trematodes) rather than species-level richness. We calculated proportional parasite prevalence as: n_i/n , where n_i = number of infected individuals and n = number of total individuals, con-

Table 2. *Carcinus maenas* and *Hemigrapsus sanguineus*. Field locations, sample sizes (crab n), and parasite diversity for field work included in the present investigation. Parasite diversity is for major parasite taxa groupings (see 'Materials and methods'). Prevalence (%) can add up to more than 100 at a site due to multiple infections of parasites within individual crabs. nd: no prevalence data available

Site	Crab (n)	Prevalence (%)							
		Acanthocephalan	Cestode	Isopod	Microsporan	Nematode	Nemertean	Rhizocephalan	Trematode
<i>Carcinus maenas</i>									
Native									
Hillesøy, Norway ^b	18	50	0	0	nd	0	11	0	100
Kristineberg, Sweden ^a	21	24	0	0	nd	0	95	7	62
Den Helder, Netherlands ^a	19	47	0	0	nd	0	26	0	74
IJmuiden, Netherlands ^a	20	20	0	0	nd	0	5	0	0
Plymouth, England ^b	20	0	0	10	0	0	0	0	85
Roscoff, France ^a	83	0	0	0	nd	0	0	6	100
Saint-Pol-de-Léon, France ^a	22	0	0	5	nd	0	0	59	100
Arcachon, France ^b	15	0	0	0	nd	0	0	0	93
Arcade, Spain ^b	20	0	0	0	55	0	0	63	100
Laguna Baldaio, Spain ^b	40	0	0	0	0	0	15	0	100
Baiona, Spain ^b	24	0	0	0	0	0	0	0	88
Vigo, Spain ^a	48	0	85	0	0	0	0	78	73
Cádiz, Spain ^b	24	0	0	0	50	0	0	0	100
Palmones, Spain ^b	27	0	0	0	44	0	0	0	100
Praia de Grandarío, Spain ^b	33	0	3	0	0	0	0	78	24
Mira River, Portugal ^b	62	11	8	3	0	0	2	19	80
Introduced									
Appledore Island, Maine ^c	31	3	0	0	0	6	0	0	100
Adams Point, New Hampshire ^c	30	3	0	0	0	0	0	0	3
Manomet, Massachusetts ^a	33	18	0	0	0	0	0	0	100
Barn Island Marsh, Connecticut ^a	22	0	0	0	0	0	0	0	0
Mason Island, Connecticut ^a	10	0	0	0	0	0	0	0	10
Rocky Neck Park, Connecticut ^b	12	0	0	0	0	0	0	0	75
Saybrook, Connecticut ^b	13	0	0	0	0	0	0	0	0
Stonington, Connecticut ^a	55	0	0	0	0	0	0	0	65
Weekapaug, Rhode Island ^a	42	0	0	0	0	0	0	0	36
Ocean City, Maryland ^b	18	0	0	0	0	11	0	0	0
<i>Hemigrapsus sanguineus</i>									
Native									
Oshoro, SW Hokkaido ^b	20				0	0		5	25
Usujiri, SE Hokkaido ^b	61				30	0		20	87
Asamushi, North Honshu ^b	20				0	0		0	55

Field data for *C. maenas* from: ^athe Torchin et al. (2001) data, ^bthe previously unpublished data collected by M.E.T., A.M.K., and K.D.L., and ^cour new data (see 'Materials and methods')

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Table 2 (continued)

Site	Crab (n)	Prevalence (%)							
		Acanthocephalan	Cestode	Isopod	Microsporan	Nematode	Nemertean	Rhizocephalan	Trematode
Otsuchi, North Honshu ^b	20				0	0		0	40
Gyotoku, Tokyo Bay ^b	16				0	0		0	63
Misake, Sagami Bay ^b	26				0	0		8	15
Tateyama, Chiba Peninsula ^b	18				0	0		0	39
Introduced									
Appledore Island, Maine ^c	19				0	0		0	0
Gloucester, Massachusetts ^c	15				0	0		0	0
Edgartown, Massachusetts ^c	22				0	0		0	0
Weekapaug, Rhode Island ^c	30				0	0		0	0
Rye Playlands, New York ^c	13				0	15		0	0
Lewes, Delaware ^c	18				0	11		0	0
Ocean City, Maryland ^c	22				0	18		0	0

Field data for *C. maenas* from: ^athe Torchin et al. (2001) data, ^bthe previously unpublished data collected by M.E.T., A.M.K., and K.D.L., and ^cour new data (see 'Materials and methods')

verting prevalence values to percentages. Because castrating and trophically transmitted parasites (which include trematodes) have different effects on host fitness, we further divided our parasite prevalence data into these 2 major parasite groupings, following the approach of Torchin et al. (2001).

Because sampling effort for each crab species and region were not equal in our study, we performed 2 standardization techniques to account for the differences in sampling effort. These standardization analyses included published (Torchin et al. 2001), previously unpublished (M.E.T., A.M.K., K.D.L.), and new field data (all presented in Table 2). Firstly, we constructed species rarefaction curves that depict species accumulation and species estimation (i.e. Chao2 estimator) with sampling effort (in EstimateS 8.0; Colwell 2006). Because clearly asymptoting accumulation curves suggest complete capture of the total species richness in a population (Gotelli & Colwell 2001), estimator curves and species accumulation curves converging on the same asymptote reflect adequate sampling (Walther & Morand 1998, Blakeslee & Byers 2008). We therefore used this technique to determine whether our sampling had been adequate across crab species and populations, or whether differences in sampling effort and area would impact our observed species richness comparisons. Specifically, we used the Chao2 estimator because it has been shown to be robust in many systems and advocated for parasite studies (Walther & Morand 1998); the Chao2 bias-corrected equation (see Colwell 2006) is:

$$\hat{S}_{\text{Chao2}} = S_{\text{obs}} + \frac{m-1}{m} \times \frac{Q_1(Q_1-1)}{2(Q_2+1)}$$

where \hat{S}_{Chao2} is the species richness estimate; S_{obs} is the total number of species observed in all samples pooled; m is the total number of samples; Q_1 is the frequency of uniques (species that occur in only 1 sample); and Q_2 is the frequency of duplicates (species that occur in only 2 samples). For our investigation, 'samples' were sample sites. Although our data were sample-based, we rescaled our species accumulation curves to accumulated individuals (see Fig. 3) in order to compare species richness across our data sets in a standardized manner (Gotelli & Colwell 2001). Secondly, we used Monte Carlo resampling (in EstimateS 8.0; Colwell 2006) to standardize sample sizes across populations and crab species at the lowest common sample size ($n = 15$ crabs) for a site and adjusted our richness values for each site based on the results of the analysis. We then used these site-level parasite richness values to compare crab species across populations using Student's pairwise t -tests (significance was determined at $\alpha = 0.05$).

Although our comparisons of site-level parasite richness standardize for sampling effort and overall regional sample size when comparing native and non-native crab populations, we performed an additional conservative analysis for *Carcinus maenas*. This was because we sampled a much larger geographic range of *C. maenas* on the European coast compared to the US East Coast (in contrast, the sampled native and non-native regions for *Hemigrapsus sanguineus* were of similar geographic sizes). We therefore examined a subset of our *C. maenas* data from a central/western sampling region (6 sites: Arca-chon, France; Saint-Pol-de-Léon, France; Roscoff, France; Plymouth, England; IJmuiden, Netherlands; and Den Helder, Netherlands) over a geographic size (~1000 km) that was more similar (using a rough, linear distance) to the US East Coast range (~700 km) we investigated. We focused on this central region of the European range for 2 reasons: (1) our sample sites on the US East Coast were also primarily from the central region of the crab's range (which extends from Virginia, USA, to Newfoundland, Canada) and overlap the region where the crab was initially introduced and rapidly spread in the 19th century (Carlton & Cohen 2003); (2) the European source region for *C. maenas*' introduction overlaps much of the western European area we included in our subset (i.e. sites southwest of Bremerhaven, Germany; Roman 2006). Of note, however, is that these comparative ranges (the native subset region and the introduced region) are latitudinally different; exploring similar latitudes would have represented only the southern portion of the crab's European range.

RESULTS

Carcinus maenas

In its native European range, *Carcinus maenas* is infected by 10 parasite species compared to 3 in its introduced US East Coast range (Table 1), and the crab's proportional parasite escape is 0.70. All parasites found on the East Coast were a subset of the European parasite fauna, except for an (as yet) unidentified larval nematode on the East Coast. This may be

the same nematode reported in Torchin et al. (2001) for both *C. maenas* and *Hemigrapsus sanguineus*. Overall prevalence of infection in native European populations was 24% for castrating parasites and 89% for trophically transmitted parasites (summed parasite prevalence can be greater than 100% due to dual infections in both categories), while for introduced East Coast populations, castrating parasite prevalence was 0% and trophically transmitted parasite prevalence was 49% (Fig. 2a). At the site level, average prevalences were similar to the overall prevalences for both native and introduced populations (Fig. 2b). Altogether, parasite prevalence (primarily dominated by trematode infections) in the introduced range was approximately half that of the native European range (Fig. 2). While sampling effort was not equal across populations, our rarefaction analyses found the total expected parasite richness to be equivalent to the observed richness values for both native and introduced regions (Fig. 3a,b), suggesting that sampling was adequate to capture the

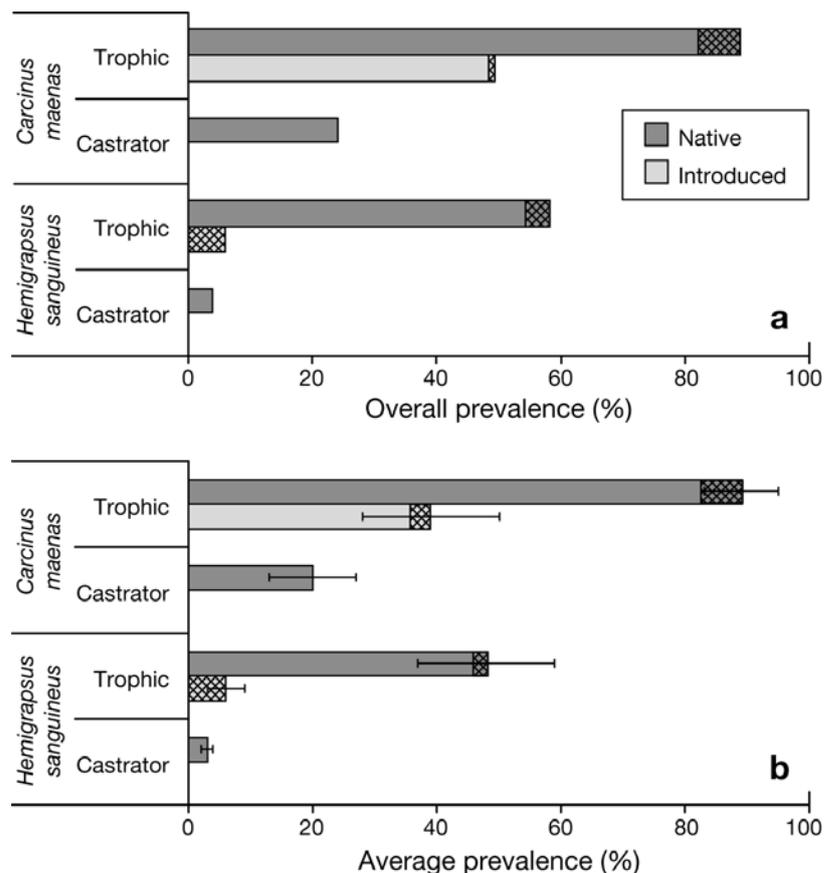


Fig. 2. Prevalence in *Carcinus maenas* and *Hemigrapsus sanguineus* for native and introduced regions of the 2 parasite groupings (castrator and trophic): (a) overall prevalence; (b) average site-level prevalence. Stacked bars represent proportion of metacercaria (trematode) and non-metacercaria infections within trophically transmitted prevalence (cross hatching = non-metacercaria prevalence). Data included in prevalence analyses are from field records (see 'Materials and methods')

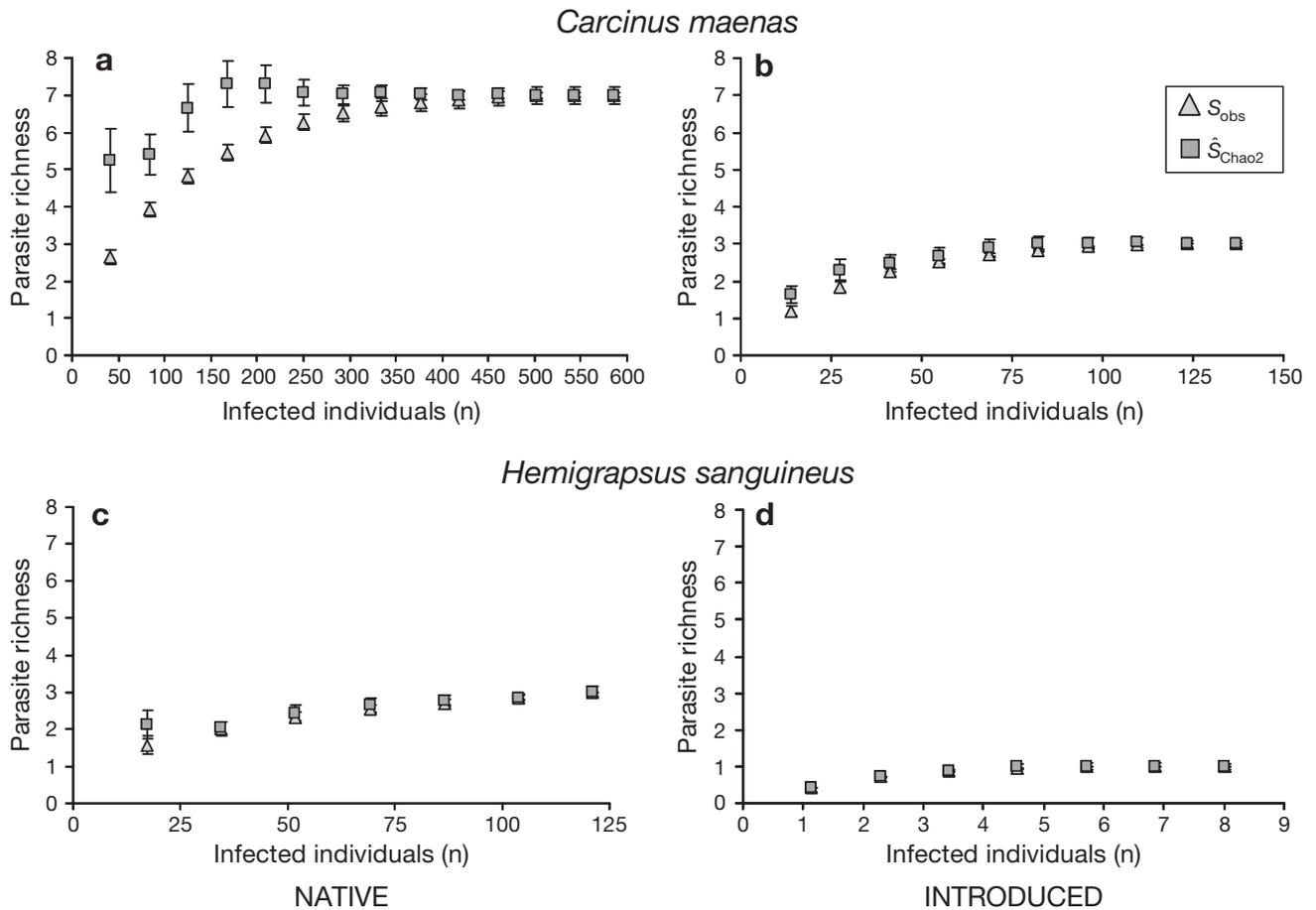


Fig. 3. Parasite rarefaction curves for (a,b) *Carcinus maenas* and (c,d) *Hemigrapsus sanguineus* in native and introduced regions. Curves portray the accumulation of parasites (number of species observed, S_{obs}) and the expected parasite richness (\hat{S}_{Chao2}) as a function of the number of infected individuals in each population and for each crab species. Error bars (some error bars are small and difficult to discern) are SE for 500 runs in EstimateS (Colwell 2006), and data were from field records only (see 'Materials and methods'). These analyses not only demonstrate each crab's parasite escape but also that sampling effort (though not equal) adequately reflected underlying richness in each population

underlying parasite richness in native and introduced populations. Our second standardization method used a Monte Carlo resampling analysis to explore average (\pm SE) parasite richness across sites and resulted in a site-level richness of 2.31 ± 0.22 in Europe compared to 1.38 ± 0.15 on the US East Coast, which was a significant reduction ($p = 0.013$) (Fig. 4, Appendix 1). In the analysis where we explored a subset of our European field data, we found total species richness to be 6 taxa in Europe as opposed to 3 on the US East Coast, representing a parasite escape of 0.50. Parasite prevalence averaged (\pm SE) across the 6 sites was $10.8 \pm 9.7\%$ for castrating parasites and $78.8 \pm 12.4\%$ for trophically transmitted parasites. When these results were compared to those from the US East Coast, *C. maenas* continued to show a large reduction (close to half that of Europe) in prevalence in its introduced range compared to the subset we explored in its native range.

Hemigrapsus sanguineus

Hemigrapsus sanguineus is infected by 6 parasite species in its native Asian range compared to 1 in its introduced US East Coast range (Table 1), and the crab's escape from parasites is 0.83. In Asia, overall parasite prevalence was 4% for castrating parasites and 58% for trophically transmitted parasites, and on the US East Coast, prevalence was 0% for castrating parasites and 6% for trophically transmitted parasites (Fig. 2a); site-level average prevalence in both regions was again similar to the crab's overall prevalence (Fig. 2b). On the whole, parasite prevalence in the introduced US range was about 90% lower than native Asia (Fig. 2) and was represented by only 1 parasite taxon (larval nematode). Interestingly, we found this nematode to be limited to the southern areas of its sampled range (Rye, NY, and southwards; see Fig. 1), which is within the general area of its initial founding region.

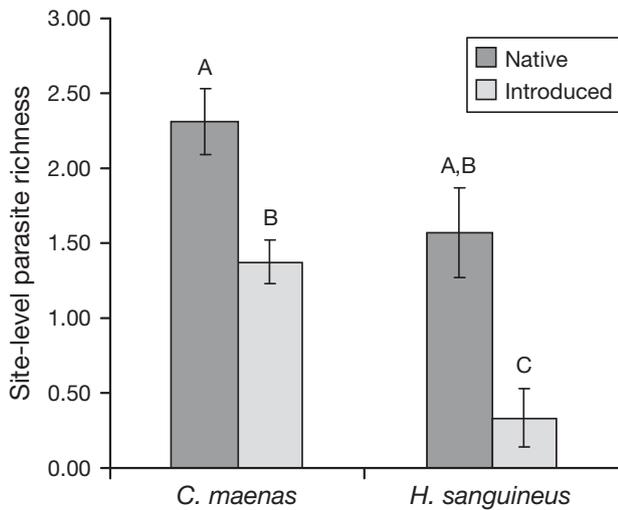


Fig. 4. *Carcinus maenas* and *Hemigrapsus sanguineus*. Standardized site-level parasite richness for taxa in native and introduced populations across sites. Data included in these analyses are from field records only and richness was standardized (Appendix 1) using a Monte Carlo resampling analysis (see 'Materials and methods'). Significance values (A, B, C) are based on pairwise comparisons from Student's *t*-tests

Sample size was again unbalanced between the regions; yet our species rarefaction curves found that the total expected parasite richness was equivalent to the observed richness values in both regions (Fig. 3c,d). Finally, standardization of our Asian and East Coast field data resulted in the average (\pm SE) site-level parasite richness for Asian sites to be 1.57 ± 0.30 and for US East Coast sites to be 0.33 ± 0.20 , a significant reduction ($p = 0.011$) (Fig. 4, Appendix 1).

Comparison of crab species

The magnitude of escape from parasites differed between the 2 crab species. Altogether, *Hemigrapsus sanguineus*' escape from parasites (0.83) was 1.2 times greater than that of *Carcinus maenas* (0.70) when including field and literature data. Furthermore, the reduction in parasite prevalence in introduced versus native populations was about twice as great for *H. sanguineus* as for *C. maenas*, e.g. Fig. 1 visually displays this overall reduction in parasite prevalence in the introduced range compared to both crabs' native ranges, especially for *H. sanguineus*, where the majority of sites had zero prevalence. Comparing just within the introduced East Coast range, parasite prevalence in *H. sanguineus* was more than an order of magnitude lower than prevalence in *C. maenas* (Fig. 2) and *H. sanguineus* had a significantly ($p = 0.025$) lower parasite richness than did *C. maenas* in their overlapping

introduced range (Fig. 4). Overall, our standardization techniques imply that we approached complete capture of parasite richness in all populations and for both crab species (Figs. 3 & 4), suggesting sampling bias was unlikely to contribute to the differences we observed between the 2 crab species. When we compared our *H. sanguineus* data set to the *C. maenas* subset data set (i.e. the subset of the European population from which *C. maenas* was most likely introduced), *H. sanguineus*' escape from parasites (0.83) was about 1.7 times greater than that of *C. maenas* (0.50), and average parasite prevalence was again about twice as reduced for *H. sanguineus* as for *C. maenas* in introduced versus native ranges.

DISCUSSION

Carcinus maenas and *Hemigrapsus sanguineus* populations showed a significant decline in both parasite species richness and prevalence in their introduced range (the US East Coast) compared to their native ranges (Europe and Pacific Asia, respectively). However, *H. sanguineus*' escape from parasites was 1.2 times greater than that of *C. maenas* (1.7 times greater when the *H. sanguineus* data was compared to the *C. maenas* subset data), and site-level parasite richness was significantly lower for *H. sanguineus* than *C. maenas* in their overlapping introduced range along the US East Coast. Also, *H. sanguineus*' reduction in parasite prevalence was about twice that experienced by *C. maenas* in the crabs' overlapping introduced range for the whole data set as well as the European subset data. Altogether, we found *H. sanguineus* to be infected (both absolutely and proportionally) by fewer parasites on the US East Coast than *C. maenas*, which we have shown is unlikely affected by sampling bias. Moreover, it is not the case that *H. sanguineus* is restricted to areas where the parasites infecting *C. maenas* do not exist, since *H. sanguineus* overlaps with *C. maenas* in the primarily rocky intertidal habitat where these parasites were found infecting the green crab. Even when we restricted our comparison of *H. sanguineus* and *C. maenas* to sites where both species co-occurred, *C. maenas* continued to show a greater species richness and prevalence of infection than *H. sanguineus*, consistent with patterns we observed at the overall population level.

Escape of introduced populations from parasites (both richness and prevalence) is common across taxa (Torchin et al. 2002, 2003) and has been suggested as a potential advantage for introduced host species that are released from detrimental fitness effects induced by parasitic infections (e.g. Elton 1958, Dobson 1988, Byers 2000, Torchin et al. 2001). For *Carcinus maenas*,

evidence has been found demonstrating physiological and likely ecological benefits due to the crab's release from parasites in its introduced populations (Torchin et al. 2001). In particular, demographic performance (individual size and biomass) of European *C. maenas* crabs declines with increasing prevalence of parasitic castrators (which block reproduction and retard growth), and these parasitic castrators are absent in the crab's introduced East Coast population (Torchin et al. 2001). For *H. sanguineus*, it is not yet known whether the crab's escape from parasites will result in similar advantages in its introduced range. However, like *C. maenas*, *H. sanguineus* may benefit from its substantial decline in parasite infection on the US East Coast, particularly the absence of parasitic castrators, which, though relatively rare across its native range, have been found at some sites to infect the crab at high prevalences (e.g. Korn et al. 2004) and can greatly reduce its fitness (Yamaguchi et al. 1984, Takahashi & Matsuura 1994, Isaeva et al. 2001, 2005, Korn et al. 2004).

While both crabs experience a reprieve from parasitic castrators on the East Coast, *Carcinus maenas* is infected by a significantly greater prevalence and richness of tropically transmitted parasites than is *Hemigrapsus sanguineus* in this same region. In particular, *C. maenas'* most common East Coast parasite (overall prevalence of ~40%) is a tropically transmitted trematode, *Microphallus similis*, which encysts as metacercariae (often with hundreds of cysts) within the crab's tissues. Metacercarial infections (and microphallid infections in particular) have been found to damage internal tissues (Martorelli & Schuldt 1990, Robaldo et al. 1999) and impact host growth (Thieltges 2006), and can induce mortality (Meissner & Bick 1999, Fredensborg et al. 2005). While *M. similis* often occurs at high prevalence and intensity in East Coast *C. maenas* populations, our survey of the US East Coast found no natural infections of *M. similis* in *H. sanguineus*, nor could infection be induced experimentally (C.L.K. unpubl.), even though *H. sanguineus* is infected by 3 trematode species, including a microphallid, in its native range (Table 1). Although fitness effects of *M. similis* infection on crab hosts have not yet been investigated, *M. similis* may confer similar fitness disadvantages as those induced by other microphallids infecting other crustacean hosts (e.g. Martorelli & Schuldt 1990, Robaldo et al. 1999). Such a scenario could play a role in the green crab's displacement by its healthier competitor, *H. sanguineus*. In particular, *H. sanguineus* can be more aggressive than *C. maenas* and often wins competitive interactions between the species (e.g. Jensen et al. 2002, Griffen & Williamson 2008). Parasitism could directly alter the behavior of heavily infected crabs (i.e. unhealthy crabs may not be as

aggressive), potentially influencing these interactions. On the other hand, infection status may not directly influence the competitive abilities of the crabs per se, but rather, operating indirectly, i.e. by differentially reducing fecundity or increasing mortality of one competitor species, they may free up more resources for the other species (Byers & Goldwasser 2001).

As we have described, *Carcinus maenas* is infected by a greater richness and prevalence of parasites on the US East Coast than *Hemigrapsus sanguineus*, and there are several potential non-mutually exclusive explanations for this observation. (1) Susceptibility: *C. maenas* may be more susceptible to parasitism than *H. sanguineus*, either because its biology and/or ecology put it in greater contact with parasites, or because it is physiologically more susceptible. (2) Time since introduction: *C. maenas* has been present on the US East Coast for almost 2 centuries while *H. sanguineus* only invaded within the last 2 decades. This increases opportunities for both the invasion of other parasites from *C. maenas'* native range and the potential to become infected by native East Coast parasites. Torchin & Lafferty (2008) found a significant linear relationship (explaining 83% of the variability in the number of parasite species in introduced populations) between age of introduced populations and parasite species richness, specifically for *C. maenas* in its various introduced populations around the world. (3) Introduction vector: *C. maenas* is believed to have been introduced with rock ballast (Roman & Darling 2007), such that infected adult crabs could have been present among the crab's initial introduced population(s), while *H. sanguineus* was likely introduced as larvae in ballast water (McDermott 1998), making introduction of infected individuals very unlikely. (4) Distance from native range: *C. maenas* is a North Atlantic species, and the distance from its native range to the US East Coast is considerably closer than that of *H. sanguineus*, which is an Asian Pacific species. Thus, the relatively close proximity of the US East Coast to the European shoreline (compared to Asia) would allow for greater ease of parasite transport from the native range. Consistent with this hypothesis (and Hypothesis 2 above), *C. maenas* is only infected by one parasite in its recent introduced population on the US West Coast, where it invaded just within the last couple of decades (Torchin et al. 2001). (5) Taxonomic isolation: There are native portunid crabs that may serve as sources of parasites for *C. maenas* on the US East Coast, but there are no native grapsids in the same region as sources for parasite transfer to *H. sanguineus*. (6) Parasite identification bias: *C. maenas* parasitism has been studied to a greater degree than *H. sanguineus* over the years; however, because our rarefaction curves (Fig. 3) suggest complete capture of parasites across regions and

crab species, this scenario may not be as likely as the others. On the whole, *H. sanguineus* could remain relatively parasite-free for a long period of time because of these various factors.

Overall, our results show a significant decline in parasite richness and prevalence of infection for both crab species in their introduced range, likely providing substantial advantages for each species. However, *Hemigrapsus sanguineus* has clearly experienced a greater reprieve from parasitism on the US East Coast, which may have aided the crab in competitively displacing *Carcinus maenas* in many East Coast populations. The reduction in *C. maenas* abundance has likely had (and is currently having) considerable community-wide impacts, including predatory influences (DeGraaf & Tyrrell 2004, Griffen et al. 2008, Griffen & Byers 2009), competitive impacts with native crab species (Lohrer & Whitlatch 2002), and it may also influence cascading effects in areas where *H. sanguineus* has become the dominant shorecrab. For example, displacement of *C. maenas* will likely impact parasite communities, especially trophically transmitted parasites using the green crab as a host for larval stages. The possible extirpation or drastic reduction of these relatively host-specific parasites could actually benefit native hosts to the extent that these hosts are involved in parasite life cycles involving *C. maenas*. For example, the trematode *Microphallus similis* uses native littorine snails, *Littorina saxatilis* and *L. obtusata*, as first-intermediate hosts on the US East Coast (Blakeslee & Byers 2008). The competitive exclusion of *C. maenas* by *H. sanguineus* could result in lower *M. similis* infection prevalences in these snails (potentially advantageous since *M. similis* castrates snail hosts). Such a scenario has been shown on the US West Coast, where an introduced snail, *Batillaria attramentaria* (Asian mudsnail), is competitively displacing the native California horn snail *Cerithidea californica* in several west coast populations. The native snail is infected by 10 trematode parasites, while in this same region, the non-native snail, *B. attramentaria*, is infected by just one morphologically distinct trematode species (also a non-native). (Of note, however, is that this trematode species has recently been found to be a complex of multiple genetically distinct cryptic species, 3 of which invaded the west coast with *B. attramentaria*; Miura et al. 2006). With the exclusion of *C. californica* by *B. attramentaria*, it is believed the 10 native parasites will go locally extinct, likely impacting other hosts (including crustaceans, mollusks, fish, and mammals) involved in the trematode life cycles (Torchin et al. 2005). Similar community-wide effects might also occur on the US East Coast where *H. sanguineus* is presently displacing *C. maenas* (although dissimilar from the example above, this system involves a non-native replacing

another non-native species). On the whole, our investigation underscores not just that non-native species lose parasites upon introduction, but that they may do so differentially, with ramifications for their direct interactions and with potential community-level influences.

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Appendix 1. Site locations, sample sizes, parasite richness, and standardized site-level species richness (adjusted richness) for parasite taxa in native (*Carcinus maenas*: Europe; *Hemigrapsus sanguineus*: Asia) and introduced (both crabs: US East Coast) populations. Adjusted richness values were based on a Monte Carlo sampling technique at the lowest common number of crabs ($n = 15$) (see 'Materials and methods'). In one case, sites were lumped together due to their close proximity (Rocky Neck and Saybrook, CT). Only sites with 15 crabs or more are included in adjusted richness analyses (thus these analyses excluded one site: Rye Playlands, NY, for *H. sanguineus*). Data included in these analyses were from field records (see 'Materials and methods')

Sites	Sample size	Richness	Adjusted richness
<i>Carcinus maenas</i>			
Europe			
Hillesøy, Norway	18	3	3
Kristineberg, Sweden	21	4	3
Den Helder, Netherlands	19	3	3
IJmuiden, Netherlands	20	2	1
Plymouth, England	20	2	2
Roscoff, France	83	2	2
Saint-Pol-de-Léon, France	22	3	3
Arcachon, France	15	1	1
Arcade, Spain	20	3	3
Laguna Baldaio, Spain	40	2	2
Baiona, Spain	24	1	1
Vigo, Spain	48	3	3
Cádiz, Spain	24	2	2
Palmones, Spain	27	2	2
Pria Gandarío, Spain	33	3	2
Mira River, Portugal	62	6	4
US East Coast			
Appledore Island, Maine	31	3	3
Adams Point, New Hampshire	30	2	2

Appendix 1 (continued)

Sites	Sample size	Richness	Adjusted richness
Manomet, Massachusetts	33	2	2
Weekapaug, Rhode Island	42	1	1
Stonington, Connecticut	55	1	1
Barn Island Marsh, Connecticut	22	0	0
Rocky Neck and Saybrook, Connecticut	25	1	1
Ocean City, Maryland	18	1	1
<i>Hemigrapsus sanguineus</i>			
Asia			
Oshoro, SW Hokkaido	20	2	2
Usujiri, SE Hokkaido	61	3	2
Asamushi, North Honshu	20	1	1
Otsuchi, North Honshu	20	1	1
Gyotoku, Tokyo Bay	16	1	1
Misake, Sagami Bay	26	2	2
Tateyama, Chiba Peninsula	18	1	1
US East Coast			
Appledore Island, Maine	19	0	0
Gloucester, Massachusetts	15	0	0
Edgartown, Massachusetts	22	0	0
Weekapaug, Rhode Island	30	0	0
Lewes, Delaware	18	1	1
Ocean City, Maryland	22	1	1

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