

META-ANALYSIS



Marine range shifts and species introductions: comparative spread rates and community impacts

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ABSTRACT

Aim Shifts in species ranges are a predicted and realized effect of global climate change; however, few studies have addressed the rates and consequence of such shifts, particularly in marine systems. Given ecological similarities between shifting and introduced species, we examined how our understanding of range shifts may be informed by the more established study of non-native species introductions.

Location Marine systems world-wide.

Methods Database and citation searches were used to identify 129 marine species experiencing range shifts and to determine spread rates and impacts on recipient communities. Analyses of spread rates were based on studies for which post-establishment spread was reported in linear distance. The sizes of the effects of community impacts of shifting species were compared with those of functionally similar introduced species having ecologically similar impacts.

Results Our review and meta-analyses revealed that: (1) 75% of the range shifts found through the database search were in the poleward direction, consistent with climate change scenarios, (2) spread rates of range shifts were lower than those of introductions, (3) shifting species spread over an order of magnitude faster in marine than in terrestrial systems, and (4) directions of community effects were largely negative and magnitudes were often similar for shifters and introduced species; however, this comparison was limited by few data for range-shifting species.

Main conclusions Although marine range shifts are likely to proceed more slowly than marine introductions, the community-level effects could be as great, and in the same direction, as those of introduced species. Because it is well-established that introduced species are a primary threat to global biodiversity, it follows that, just like introductions, range shifts have the potential to seriously affect biological systems. In addition, given that ranges shift faster in marine than terrestrial environments, marine communities might be affected faster than terrestrial ones as species shift with climate change. Regardless of habitat, consideration of range shifts in the context of invasion biology can improve our understanding of what to expect from climate change-driven shifts as well as provide tools for formal assessment of risks to community structure and function.

Keywords

Climate change, exotic species, introduced species, invasion, invasion impacts, invasive, marine systems, non-indigenous species, range shift, spread rate.

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INTRODUCTION

Humans are having unprecedented impacts on the earth's biogeochemical cycles and climate (Vitousek *et al.*, 1997), including the increase in global temperatures of $0.74 \pm 0.18^\circ\text{C}$ during the 20th century (IPCC, 2007a). Overall warming of between 2.0 and 4.5°C is predicted in the next century (IPCC, 2007a). 'Fingerprints' of recent climate changes have already been observed in biological systems. Meta-analyses by Parmesan & Yohe (2003) and Root *et al.* (2003) uncovered significant advances in spring-time phenologies (e.g. migration, flowering, spawning and larval recruitment) and poleward range shifts of species. The Intergovernmental Panel on Climate Change recently confirmed that range shifts have been widespread and stated that 'the overwhelming majority of studies of regional climate effects on terrestrial species reveal consistent responses to warming trends, including poleward and elevational range shifts of flora and fauna' (IPCC, 2007b). Although modern range shifts have also been observed in marine systems (e.g. Southward *et al.*, 1995; Oviatt, 2004; Perry *et al.*, 2005), they have received much less study (but see Fields *et al.*, 1993, for examples of range shifts associated with glacial cycles). In addition, few studies in any system have addressed the community- or species-level effects of climate-driven range shifts, and impact studies are considered by some to be the 'next frontier' in climate change research (Kintisch, 2008).

We propose that there are predictable similarities and differences between range shifts, which we define as any changes in the distributions of native species that are not directly human mediated, and human-assisted invasions. Introductions of non-native species are widespread, and non-native species have come to dominate the communities in some systems (Vitousek *et al.*, 1997; Cohen & Carlton, 1998). Introduced species are recognized as one of the main anthropogenic threats to biological systems (Sala *et al.*, 2000) and are well studied, particularly relative to range shifts. For example, studies of introduced species were five times as numerous as range-shift studies in 2007 as revealed in a preliminary database search we performed using ISI Web of Knowledge BIOSIS Previews. Introductions have come to be considered inadvertent experiments which give insights into general ecological processes (Sax *et al.*, 2005, 2007). Therefore, the study of range shifts may be informed by the more established study of species introductions (also see Dunstan & Bax, 2007).

Range shifts of native species and introductions of non-native species are analogous in that both are fundamentally biological invasions, involving the movement of individuals from a donor community into a recipient community. We differentiate between shifts and introductions as follows. Range shifts are the expansion, contraction, or both, of a species' range. In this study, we are concerned with the expansion phase of a shift, whereby a species moves into a new, adjacent location for a variety of reasons including changes in global temperature, as discussed above. Species introductions are defined as being directly mediated by humans who deliberately or inadvertently introduce non-native species to locations that they would be unlikely to

reach on their own. The introduction process can be divided into the chronological phases of inoculation, establishment and colonization or secondary spread.

In the literature, 'invasion' studies do not always differentiate between native and non-native species (e.g. Levine *et al.*, 2004; Zeidberg & Robison, 2007). The crucial difference, having ecological and evolutionary implications, is that primary donor and initially colonized recipient communities are regionally *adjacent* in range shifts but distant and *separated* in introductions (Chapman & Carlton, 1991). The degree of separation between donor and recipient communities in part determines the ecological success of range-shifters and introduced species. In this context, ecological success may include the establishment of a permanent population, increased abundance, and, sometimes, range extension beyond the initial colonization site. When using range extension as a measure of success, we focus on introduction spread rates measured during the colonization phase of secondary spread from the locale of initial establishment in order to compare parallel (non-human-assisted) spread processes for shifts and introductions. We start by developing some predictions about how shifts and introductions will compare based on examples in the biological invasion literature of the relative advantages and disadvantages of separation from the donor community that can be modified for range shifts (Fig. 1).

Separation of the recipient community from the donor community can afford ecological advantages to non-native species due to a lack of shared evolutionary history with species in the recipient community. For example, one of the most highly cited explanations for introduction success is the enemy-release hypothesis (ERH). The ERH states that introduced species are successful because they have left their coevolved natural enemies behind in the donor community and are 'safe', relative to native prey, from naïve predators in the recipient community (see meta-analyses by Colautti *et al.*, 2004, and Liu & Stiling, 2006). Similarly, the competitive release hypothesis (CRH; also called the Evolution of Increased Competitive Ability) predicts release from competition in habitats with novel competitors (Blossey & Nötzold, 1995) or no competitors. Associated with both the ERH and CRH is the hypothesis that introduced species are more successful *as* predators, in addition to suffering less predation and parasitism in their recipient community. Success may accrue when the novel prey are less well defended against the introduced predators than are the coevolved prey in their donor community (Strauss *et al.*, 2006a; Salo *et al.*, 2007). In all three scenarios – enemy release, competitive release and naïve prey – introduced species should have greater community effects than shifting species, which are likely to share more evolutionary history with predators, prey and competitors in the adjacent range.

Alternatively, adjacent locations can also offer several ecological advantages that might predict greater success of range-shifting species. First, the biotic resistance hypothesis (BRH) predicts a disadvantage of separation: introduced species may be limited by native enemies to which they have not developed defences or competitive advantages (Colautti *et al.*, 2004; Levine *et al.*, 2004; Williams & Smith, 2007). A second advantage to

	SHIFTS	INTRODUCTIONS
DEFINITION	A shift in the distribution of native species beyond their previously recorded ranges	Translocation of species by human activity (deliberate or inadvertent) to locations they would not likely reach on their own. Secondary expansion occurs when introduced species spread from the point of initial establishment
Primary donor and recipient regions:	Tend to be adjacent and thus along corridors (such as continental shelf margins)	Tend to be distant and separated, and thus across barriers (such as oceans)
SIMILARITIES	<p>Widespread in both hemispheres</p> <p>Movement from a donor to a recipient community</p> <p>Species traits allowing spread and establishment</p> <p>Susceptible to influence of climate change</p>	
DIFFERENCES		
Overall Abiotic Environment	More likely to encounter similar physical and chemical conditions	Less likely to encounter similar physical and chemical conditions
Overall Biotic Environment	Species enter somewhat similar communities and habitats, and encounter species with which they may share a longer evolutionary and ecological history (leading to phenomena such as co-evolution of predators and prey). While more likely to encounter the same or similar predators, competitors, and prey, ERH, CRH, NPH, and BRH (see right column) are not universally excluded. Thus, native shifters may have fewer community impacts.	Species enter novel communities and sometimes novel habitats, and are more likely to encounter species with which they do not share a long evolutionary nor ecological history. Advantages of lack of shared history include: leaving predators and parasites behind (Enemy-Release Hypothesis; ERH), leaving competitors behind (Competitive-Release Hypothesis; CRH), and encountering naive prey that are less well-defended against novel (introduced) predators (Naive-Prey Hypothesis; NPH). Thus, introduced species may have more community impacts. Exceptions: Introduced species may encounter novel predators, parasites and competitors to which they (the introduced species) have not developed defenses, competitive advantages, or prey capture strategies (Biotic Resistance Hypothesis; BRH)
Propagule Pressure	Consistent, steady stream of propagules, in potentially larger numbers and of greater viability; may lead to greater genetic diversity. Exceptions: immediate donor population may possess low genetic diversity if peripherally located on leading edge of range	Sporadic stream of propagules, in potentially smaller numbers and of lower viability; may lead to less genetic diversity. Exceptions: human-mediated vectors may provide high propagule supply and diversity; introductions may also represent admixtures from multiple introductions
Propagule Pool	More likely to include species of a broad range of colonizing characteristics	More likely to involve species (such as aquarium and aquaculture taxa) that are more robust, with classic 'invasive' characteristics. Exceptions: Vectors that transport entire species pools (such as ballast water) may translocate species of a broad range of characteristics
Recipient Habitat & Community	Less likely to specifically involve regions of anthropogenic disturbance and lower diversity communities	More likely to involve regions with high levels of anthropogenic disturbance, the latter potentially leading to lower diversity
Spread Direction	Unidirectional spread is more likely for species whose boundaries are historically limited by temperature	Bidirectional spread is more likely for species that have been recently introduced and have not yet reached their thermal limits
Spread rate could be faster due to:	A closer match between environments in adjacent habitats; increased propagule pressure (numbers and viability)	A lower temperature constraint as the introduced species expand to their tolerance limits

Figure 1 Summary of similarities and differences between range shifts and introductions. Hypotheses developed in invasion biology provide a starting point for articulating hypotheses about relative spread rates and community impacts of native species range shifts.

spreading between adjacent locations is that, as shown for introduced species, new species tend to be more successful in regions where physical and chemical conditions match those in their native habitats (Pyšek, 1998; Hayes & Barry, 2008). Finally, adjacent locations provide a ready source of propagules for well-established shifter populations, and propagule pressure, or the total number and quality of individuals relocated, is one of the best predictors of introduced species establishment (Cassey *et al.*, 2005; Hayes & Barry, 2008) and faster spread rates (Mack *et al.*, 2000; Lockwood *et al.*, 2005; Roman & Darling, 2007). Adjacent habitats should, thus, offer shifting species advantages of defences to native enemies, similar habitat, barring sharp breaks in substrata availability or major biogeographical boundaries, and a steady stream of propagules from a local donor or source population.

Many determinants of establishment success are also likely to be specific to species or location. Successful shifting species may have characteristics similar to those postulated for successful introduced species, such as high dispersal rates, climatic toler-

ances and competitive abilities (Lodge, 1993; Vermeij, 1996; Nyberg & Wallentinus, 2005). On the other hand, humans might give introduced species an advantage over shifting species by transporting primarily robust species with invasive characteristics, as in the introduction of aquarium and aquaculture species (Padilla & Williams, 2004; Williams & Smith, 2007). Locations likely to allow establishment of shifting species might, as suggested for introduced species, harbour less diverse communities or be more disturbed (Lodge, 1993; Stachowicz *et al.*, 1999; Sax & Brown, 2000; Levine *et al.*, 2004; but see Didham *et al.*, 2005), although it is difficult to tease disturbance apart from the confounding effects of high propagule pressure or low native diversity to explain the invasibility of these locations (Ruiz *et al.*, 2000; Wonham & Carlton, 2005; Williams, 2007; Williams & Smith, 2007).

Increasing global temperatures could make an important difference in the relative rate of spread of shifters versus introduced species. Studies of recent range shifts suggest that the spread of these species poleward (or to higher elevations) is often limited

by temperature (Parmesan & Yohe, 2003; Root *et al.*, 2003; Parmesan, 2006). The initial spread of introduced species should be less limited by temperature because it is statistically improbable for the points of first inoculation to occur at absolute tolerance (and range) limits. Similarly, introduced species have the potential to spread bidirectionally and may be more eurythermal than shifting species (Lodge, 1993; Dukes & Mooney, 1999; Stachowicz *et al.*, 2002). Thus, from an environmental threshold perspective, initial spread of introduced species could be fast relative to spread of shifting species that are tracking changing temperature isoclines.

The conceptual framework developed above from hypotheses in invasion biology leads to a series of predictions for how spread rates and community impacts should vary between range shifts and introductions. The ERH, CRH and naïve prey hypotheses predict that introductions should have stronger effects on the recipient communities than range shifts. Introductions also might have stronger effects if humans selectively move robust, aggressive species to disturbed locations. Range shifts could proceed faster than introductions due to a closer match between adjacent habitats and to increased propagule pressure. However, if temperature sets the range boundaries of shifting species, spread rates may be constrained by rates of temperature increase. We explore these predictions through a review and meta-analyses of marine species to address the similarities and differences between range shifts and introductions. We ask the following questions:

1. What, and how many, marine species have undergone documented range shifts?
2. How fast do marine range shifts occur, and how do these spread rates compare with those for introduced species?
3. What are the impacts of range shifts on recipient marine communities, and how do the magnitudes of these impacts compare with those of introductions?

In this study, we provide the first quantitative review and analysis of marine range shifts. We show that although spread rates of marine range shifts tend to be lower than those of marine introductions, community impacts of marine range shifts and introductions are often similar.

METHODS

To identify marine species experiencing range shifts, we conducted database searches of the primary literature and examined citations in review papers. We searched the biological sciences database ISI Web of Knowledge BIOSIS Previews for topics 'range' and 'shift', 'expansion' or 'extension' from 1926 to 2008. In all searches, word roots were used to cast the widest possible net. Results were narrowed by specifying topics with marine and oceanic descriptors (including marine, ocean, saltwater, intertidal, pelagic, estuarine, mangrove, reef, subtidal, Pacific, Atlantic). In addition, we incorporated species from a running list of poleward shifts encountered in the literature over the past decade.

We considered species to be shifting based on conclusions of the studies themselves and our own evaluation. We only

included species for which evidence indicated establishment in the new range. Our search yielded many early studies that extended a species' known, but probably not actual, range (as typically acknowledged by the authors themselves). Transient reports, including those associated with El Niño, and appearances of single individuals were excluded because they did not meet the establishment criterion. Examples of repeated expansions and contractions or reintroductions were excluded (e.g. pelagic red crabs and sea otters) due to the equivocal nature of the range shift timelines and human involvement, respectively. We also excluded, due to their reliance on human activities, species that have passed through human-made canals such as the Suez Canal and Panama Canal and then spread after such passage, as well as native species that were probably transported by humans. However, we acknowledge that some expanders – like introduced species – could have spread via human vectors. To determine range shift timelines, we used establishment dates instead of those of first (often transient) sightings. When date ranges were given, we used a median date (e.g. 1975 for '1970s'). The majority of studies were dated after 1985 due to better benchmark documentation of species initial ranges.

Analyses of spread rates were based on studies of 73 species. When spread rate was not reported in the primary references, it was estimated, if possible, from degrees of latitude using the conversion: 1° latitude = 110 km. Rates of marine range shifts were compared with rates published in reviews of terrestrial shifts (Parmesan & Yohe, 2003) and marine and terrestrial introductions (Grosholz, 1996; Kinlan & Hastings, 2005). For marine introductions, we reviewed all of the species included in Kinlan & Hastings (2005) to confirm that the values were based on evidence consistent with our criteria of well-documented historical range boundaries, introduction timelines and establishment. In addition, we attempted to only include introduced species whose secondary spread was not human-mediated but, rather, occurred by the same natural processes as the spread of native range shifters. A complete list of the introduced species included in the spread rate analysis is given in Appendix S1 in Supporting Information. Rates were compared using one-way *t*-tests. Additional information about taxa represented in the spread rate analysis is available in Appendix S2.

The ecological effects of marine species undergoing range shifts were found by searching for the species names in the BIOSIS Previews database and, when publication volume was > 200 papers, the geographic location. Only studies conducted in the shifted range (between the historical and current range boundaries) were considered; studies only in native ranges were excluded.

To compare range shift and introduction impacts, we then conducted targeted searches for examples of functionally similar introduced species having ecologically similar impacts (see Appendix S3 for studies). For example, to assess impacts relative to those of a shifting predatory squid on its fish prey, we combined search strings for 'introduction' and 'marine' studies with the term 'predation'. For the general ecological effect category of 'competition', we limited our search by taxon (to primary producers) to more specifically compare examples of sessile species

competition for space and/or nutrients. In addition to conducting impact searches using BIOSIS Previews, we also found studies of impacts of introduced marine disease using Google Scholar and of impacts of introduced seaweeds in two recent comprehensive reviews (Schaffelke & Hewitt, 2007; Williams & Smith, 2007). We considered each species and study combination as a datum. Thus, data points may represent multiple impact measures of the same species (by different studies) or by the same study (of different species). For both range shifts and introductions, impacts were assessed by a variety of methods, including field observations and field and laboratory experiments. Conventions for incorporating studies of myriad designs and additional methods are provided in Appendix S4.

When necessary, we extracted data using the computer program TECHDIG v.2.0 (R. B. Jones) and contacted authors for additional data. We compared range shift and introduction impact studies by calculating the log-transformed response ratio (ln RR), a commonly used meta-analytical metric that reduces measures on variable scales to proportional values (Hedges *et al.*, 1999; Lajeunesse & Forbes, 2003). Unlike Hedge's *d*, the ln RR metric is not weighted by, and does not require knowledge of, variances and sample sizes, which were not available for all studies. This calculation yielded an effect size (ES) = $\ln [(-INV)/(+INV)]$ where '-INV' and '+INV' represent recipient community values where the shifting or introduced species was absent and present, respectively. Mean effect sizes were calculated separately for introduced species studies of each general ecological effect. Bootstrap 95% confidence intervals were determined by running 999 iterations using the jackboot macro in SAS v.9.1 (SAS Institute Inc., Cary, NC, USA). The ES values for introduced species were considered significant when the 95% bootstrap confidence intervals did not overlap zero. We conducted sensitivity analyses to confirm that our effect sizes were not solely driven by extreme values for individual species or studies. The significance and conclusions of our findings did not change when multiple values from a single species or study were condensed to a single data point.

RESULTS

We identified 129 marine species that have shifted their ranges, as documented in 55 separate studies (Table 1, Appendix S5). These include 31 primary producers (phytoplankton, macroalgae and higher plants), 24 molluscs, 36 fishes, 15 crustaceans, 10 birds, 5 cnidarians, 4 sponges and 1 species each of protist, echinoderm, annelid and insect. Most species documented as shifting were coastal; open ocean species were under-represented in range shift studies (although further analysis of large data sets, such as the Continuous Plankton Records, would be likely to yield additional oceanic species; Barnard *et al.*, 2004; Hays *et al.*, 2005). Of studies found in the database search, climate change was considered in the primary reference to be the cause of over 70% of the range shifts, and 75% of the shifts were in the poleward direction (Table 1).

Marine range shifts occurred at an average rate of 19.0 km year⁻¹ (± 3.8 SE, $n = 73$) (Fig. 2, Table 1). This rate is over an

order of magnitude faster than terrestrial range shifts (0.61 ± 0.24 km year⁻¹; $t = 5.60$, d.f. = 170, $P < 0.0001$). However, marine range shifts are over two times slower than marine introductions (44.3 ± 10.8 km year⁻¹; $t = 2.80$, d.f. = 97, $P = 0.0062$). Terrestrial introduction spread rates were slightly higher than those of marine introductions ($t = 1.97$, d.f. = 37, $P = 0.0559$). The actual average rate of marine range shifts for this subset of species is likely to be higher than values reported because the latitudinal calculation underestimates distance along nonlinear and east-west oriented coastlines.

We found evidence of community- and ecosystem-level effects for eight of the 129 shifting species (Table 2). The effects were diverse, including nutrient inputs, competition, herbivory, predation and disease. Range shift effects ranged from a 13% decrease in microalgal biomass on oyster shell substratum by the herbivorous crab *Petrolisthes armatus* (ES = -0.14) to a more than 4000% decrease in total algal biomass by the urchin *Centrostephanus rodgersii* (ES = -8.35). All eight shifting species had negative effects on the community. Even though the effect of the shifting gull *Larus delawarensis* appears as positive, because nitrogen in the soil was increased, the shift led to an increased proportion of non-native species in the community (Hogg & Morton, 1983). Because we treat the ecological effects separately, and only herbivory was replicated, our range shifter versus introduced species comparison is limited. Our targeted review of comparable introduced species studies uncovered significant effects of introduced species on native systems through competition, herbivory, predation and disease (CIs do not intersect with 0; for herbivory, comparison is based on the average of shifter values; Fig. 3). The relationship between shifter and introduced species effect sizes varied greatly with the particular ecological impact (Fig. 3). Species undergoing range shifts had the same magnitude of effects as introduced species for competition, predation and herbivory (based on the average of shifter values). Range-shifting species had higher-magnitude effects on nutrient (nitrogen) levels, but lower-magnitude effects on disease, than the suite of introduced species.

DISCUSSION

Since the mid-1990s, several seminal studies have offered suggestive evidence for marine range shifts by tracking changes in species abundances (Barry *et al.*, 1995; Southward *et al.*, 1995; Holbrook *et al.*, 1997; Beaugrand *et al.*, 2002). However, our review is the first to collate studies that documented shifts not just in the abundance but in the actual range boundaries of marine species. These 129 shifting species include myriad marine taxa, from primary producers to invertebrates to vertebrates. Our finding that 75% of the range shifts found in the database search were in the poleward direction is comparable to the result reported by Root *et al.* (2003). In their global meta-analysis of phenological and range shifts, they found that over 80% of almost 1500 terrestrial and aquatic species (with which our search shared only two species) had shifted poleward, the direction generally predicted by climate change. It is worth noting that this method of calculating poleward range shifts

Table 1 Marine native species ($n = 129$) that have undergone documented range shifts.

Taxon	Species or group	Location	Spread rate (km year ⁻¹)	Distance spread (km)	Time period	Reference
Protists	<i>Perkinsus marinus</i>	East coast, USA	78.6	1100	1988–2002	Ford & Chintala (2006)
Phytoplankton	<i>Alexandrium minutum</i>	North Atlantic	nd	nd	nd–1992	Nehring (1998)
	<i>Chattonella marina</i>	North Atlantic	nd	nd	nd–1991	Nehring (1998)
	<i>Corethron criophilum</i>	North Atlantic	nd	nd	nd–1990	Nehring (1998)
	<i>Gephyrocapsa oceanica</i>	Australia	nd	nd	nd–1992	Blackburn & Cresswell (1993)
	<i>Gymnodinium chlorophorum</i>	North Atlantic	nd	nd	nd–1990	Nehring (1998)
	<i>Neodenticula seminae</i>	North Atlantic	nd	nd	1998–99	Reid et al. (2007)
	<i>Prorocentrum redfieldii</i>	North Atlantic	nd	nd	nd–1961	Nehring (1998)
	<i>Rhizosolenia indica</i>	North Atlantic	nd	nd	nd–1989	Nehring (1998)
	<i>Stephanopyxis palmeriana</i>	North Atlantic	nd	nd	nd–1990	Nehring (1998)
	Seaweeds	<i>Ahnfeltia plicata</i>	Portugal	6.7	330	1955–2004
<i>Bifurcaria bifurcata</i>		Britain and Ireland	3.9	150	1964–2002	Mieszkowska et al. (2005)
<i>Bifurcaria bifurcata</i>		Portugal	5.2	257	1955–2004	Lima et al. (2007)
<i>Chondrus crispus</i>		Portugal	3.7	180	1955–2004	Lima et al. (2007)
<i>Codium adhaerens</i>		Portugal	1.2	59	1955–2004	Lima et al. (2007)
<i>Desmarestia aculeata</i>		Portugal	4.6	227	1955–2004	Lima et al. (2007)
<i>Desmarestia ligulata</i>		Portugal	1.4	70	1955–2004	Lima et al. (2007)
<i>Dumontia contorta</i>		Portugal	1.3	62	1955–2004	Lima et al. (2007)
<i>Fucus serratus</i>		Spain	5.0	100	nd	Arrontes (2002)
<i>Fucus vesiculosus</i>		Portugal	3.2	157	1955–2004	Lima et al. (2007)
<i>Halidrys siliquosa</i>		Portugal	1.8	90	1955–2004	Lima et al. (2007)
<i>Halopithys incurva</i>		Portugal	9.7	475	1955–2004	Lima et al. (2007)
<i>Himanthalia elongata</i>		Portugal	4.5	219	1955–2004	Lima et al. (2007)
<i>Hypnea musciformis</i>		Portugal	5.5	269	1955–2004	Lima et al. (2007)
<i>Padina pavonica</i>		Portugal	3.8	187	1955–2004	Lima et al. (2007)
<i>Palmaria palmata</i>		Portugal	7.3	358	1955–2004	Lima et al. (2007)
<i>Pelvetia canaliculata</i>		Portugal	5.0	245	1955–2004	Lima et al. (2007)
<i>Sargassum flavifolium</i>		Portugal	12.1	593	1955–2004	Lima et al. (2007)
<i>Turbinaria ornata</i>		French Polynesia	8.0	200	1980–2005	Stewart (2008)
<i>Valonia utricularis</i>		Portugal	4.0	197	1955–2004	Lima et al. (2007)
<i>Zanardinia prototypus</i>	Britain and Ireland	55.0	165	1975–78	Hiscock & Maggs (1982)	
Plants	<i>Avicennia germinans</i>	Gulf coast, USA	13.0	65	1980–85	Sherrod & McMillan (1981)
	<i>Rhizophora mangle</i>	Florida, USA	nd	65	nd–2005	Zomlefer et al. (2006)
Sponges	<i>Chalinula loosanoffi</i>	NE coast, USA	15.4	385	1950–75	Perkins & Larsen (1975)
	<i>Halichondria bowerbanki</i>	NE coast, USA	19.3	385	1950–70	Bleakney & Mustard (1974)
	<i>Haliclona canaliculata</i>	NE coast, USA	17.6	440	1950–75	Perkins & Larsen (1975)
	<i>Hexadella racovitzai</i>	Ireland	35.8	715	1985–2005	Picton & Goodwin (2007)
Hydroids	<i>Abietinaria filicula</i>	Europe	nd	nd	nd	Cornelius (1995)
Corals	<i>Acropora cervicornis</i>	Florida, USA	6.3	82.5	1985–98	Precht & Aronson (2004)
	<i>Acropora palmata</i>	Florida, USA	9.7	165	1985–2002	Precht & Aronson (2004)
	<i>Astroides calycularis</i>	Mediterranean Sea	15.7	330	1980–2001	Bianchi (2007)
Sea jellies	<i>Aglantha digitalis</i>	England	5.5	55	1969–79	Southward et al. (1995)
Bivalves	<i>Nuttallia nuttallii</i>	California, USA	6.8	402	1945–2004	Yoshimoto (2004)
	<i>Pseudochama exogyra</i>	California, USA	nd	165	nd–1975	Coan et al. (2000)
	<i>Mytilus edulis</i>	Norway	62.5	500	nd	Berge et al. (2005)
	<i>Mytilus edulis</i>	Norway	29.4	500	nd	Weslawski et al. (1997)
Chitons	<i>Enoplochiton niger</i>	Chile	7.7	385	nd	Rivadeneira & Fernandez (2005)
Gastropods	<i>Bulla gouldiana</i>	California, USA	nd	330	nd–1975	McLean (2007)
	<i>Creedonia succinea</i>	SE coast, USA	nd	715	nd–1996	Harrison & Knott, 2007
	<i>Glossaulax reclusianus</i>	California, USA	nd	440	nd–1975	McLean (2007)
	<i>Lacuna unifasciata</i>	California, USA	nd	165	nd–2003	McLean (2007)
	<i>Microtralia ovula</i>	SE coast, USA	nd	495	nd–1976	Harrison & Knott (2007)
	<i>Spurwinkia salsa</i>	Canada	7.0	280	1964–2004	McAlpine et al. (2005)
	<i>Acanthimucella spirata</i>	California, USA	nd	440	12,000–30,000 BP	Hellberg et al. (2001)
	<i>Echinolittorina peruviana</i>	Chile	14.9	550	nd	Rivadeneira & Fernandez (2005)
	<i>Fissurella crassa</i>	Chile	8.9	330	nd	Rivadeneira & Fernandez (2005)
	<i>Gibbula umbilicalis</i>	Britain and Ireland	3.2	55	1985–2002	Mieszkowska et al. (2005)
	<i>Kelletia kellestii</i>	California, USA and Mexico	32.5	325	nd	Zacherl et al. (2003)
	<i>Lottia orbigny</i>	Chile	13.8	330	nd	Rivadeneira & Fernandez (2005)
	<i>Norrissia norrisi</i>	California, USA	nd	432	nd	Lonhart & Tupen (2001)
	<i>Osilinus lineatus</i>	Britain and Ireland	3.4	55	1986–2002	Mieszkowska et al. (2005)
	<i>Patella depressa</i>	Britain and Ireland	1.3	30	1985–2004	Mieszkowska et al. (2005)
	<i>Patella ulyssiponensis</i>	Britain and Ireland	5.0	120	1985–2004	Mieszkowska et al. (2005)
	<i>Scurria viridula</i>	Chile	5.9	220	nd	Rivadeneira & Fernandez (2005)
	<i>'Lottia' depicta</i>	California, USA	nd	nd	nd	Zimmerman et al. (1996)
	<i>Thais haemastoma</i>	Chile	15.9	825	nd	Rivadeneira & Fernandez (2005)

Table 1 Continued

Taxon	Species or group	Location	Spread rate (km year ⁻¹)	Distance spread (km)	Time period	Reference
Squids	<i>Dosidicus gigas</i>	USA west coast	199.4	1595	1997–2005	Brodeur <i>et al.</i> (2006)
Sea urchins	<i>Centrostephanus rodgersii</i>	Australia	16.5	330	1965–85	Ling <i>et al.</i> (2008)
Annelids	<i>Diopatra neapolitana</i>	Europe	3.6	300	1923–2006	Wetthey & Woodin (2008)
Amphipods	<i>Caprella scaura</i>	SE coast, USA	nd	nd	nd	Foster <i>et al.</i> (2004)
Copepods	Calanoid assemblages	North Atlantic	28.2	1100	1960–99	Beaugrand <i>et al.</i> (2002)
Euphausiids	<i>Thysanoessa inspinata</i>	Alaska, USA	33.0	990	1969–99	Lindley <i>et al.</i> (2004)
Barnacles	<i>Balanus perforatus</i>	England	5.2	170	1964–97	Herbert <i>et al.</i> (2003)
	<i>Chthamalus montagui</i>	Britain and Ireland	2.6	140	1955–2003	Mieszkowska <i>et al.</i> (2005)
	<i>Chthamalus montagui</i>	England and France	1.3	50	1955–95	Herbert <i>et al.</i> (2007)
	<i>Chthamalus stellatus</i>	Britain and Ireland	0.7	40	1955–2004	Mieszkowska <i>et al.</i> (2005)
	<i>Chthamalus stellatus</i>	England and France	1.3	50	1955–95	Herbert <i>et al.</i> (2007)
	<i>Semibalanus balanoides</i>	Europe	1.2	50	1965–2006	Wetthey & Woodin (2008)
	<i>Solidobalanus fallax</i>	Europe	49.0	1520	1957–88	Southward <i>et al.</i> (2004)
	<i>Tetraclita rubescens</i>	California, USA	22.0	330	1980–95	Connolly & Roughgarden (1998)
Crabs	<i>Panopeus meridionalis</i>	Argentina	4.6	55	1992–2004	Spivak & Luppi (2005)
	<i>Callinectes bocourti</i>	South Carolina, USA	45.3	770	1960–77	USGS NAS program website
	<i>Callinectes exasperatus</i>	South Carolina, USA	nd	880	nd–2002	USGS NAS program website
	<i>Eurypanopeus depressus</i>	Argentina	13.2	330	1978–2003	Spivak & Luppi (2005)
	<i>Percnon gibbesi</i>	Mediterranean Sea	nd	440	nd–1999	Relini <i>et al.</i> (2000)
	<i>Petrolisthes armatus</i>	SE coast, USA	nd	nd	nd–1995	Hollebone & Hay (2007)
Insects	<i>Coelopa pilipes</i>	Scotland and Sweden	3.7	55	1990–2005	Edward <i>et al.</i> (2007)
Fishes	6 North Sea fishes*	North Atlantic	2.2	nd	1978–2001	Perry <i>et al.</i> (2005)
	28 North Sea fishes†	North Atlantic	nd	nd	1980–2004	Dulvy <i>et al.</i> (2008)
	<i>Cymatogaster aggregata</i>	Alaska, USA	55.6	389	1998–2005	Wing (2006)
	<i>Entelurus aequoreus</i>	North Atlantic	165.0	990	1999–2005	Harris <i>et al.</i> (2007)
	<i>Hermosilla azurea</i>	California, USA	31.4	440	1981–95	Sturm & Horn (2001)
	<i>Sparisoma cretense</i>	Italy	nd	220	nd–2000	Guidetti & Boero (2001)
	<i>Thalassoma pavo</i>	Mediterranean Sea	66.0	990	1980–95	Bianchi (2007)
	<i>Zenopsis conchifer</i>	England	6.0	990	1960–95	Stebbing <i>et al.</i> (2002)
Birds	<i>Egretta garzetta</i>	Britain	nd	nd	nd–1996	Musgrove (2002)
	<i>Larus delawarensis</i>	Canada	7.4	275	1965–2002	McAlpine <i>et al.</i> (2005)
	<i>Larus hartlaubii</i>	South Africa	45.8	550	1990–2002	Crawford <i>et al.</i> (2008)
	<i>Phaethon rubricauda</i>	Australia	nd	nd	nd	Dunlop & Wooller (1986)
	<i>Phalacrocorax coronatus</i>	South Africa	29.6	355	1991–2003	Crawford <i>et al.</i> (2008)
	<i>Puffinus mauretanicus</i>	Western Europe	nd	220	nd	Wynn <i>et al.</i> (2007)
	<i>Pygoscelis adeliae</i>	Antarctica	nd	3	nd	Taylor & Wilson (1990)
	<i>Sterna anaethetus</i>	Australia	nd	nd	nd	Dunlop & Wooller (1986)
	<i>Sterna dougallii</i>	Australia	nd	nd	nd–1982	Dunlop & Wooller (1986)
	<i>Sterna forsteri</i>	California, USA	nd	380	nd–1962	Gallup (1963)

nd, no data.

*Average spread rate of 6 fish species: *Arnoglossus laterna*, *Echiichthys vipera*, *Glyptocephalus cynoglossus*, *Micromesistius poutassou*, *Trisopterus esmarkii* and *Trisopterus luscus* (Perry *et al.*, 2005).

†Four of 28 species are the same as those included in Perry *et al.* (2005).

When the spread rate was not given in the primary reference, it was estimated using the conversion 1° latitude = 110 km. Dates given under 'Time period' were averaged as stated in the Methods.

Nomenclatural authorities for all taxa are available from the Integrated Taxonomic Information System (<http://www.itis.gov>). See Appendix S5 for references.

may reflect, in part, the more frequent publication of positive results; we attempted to avoid this bias by using only species found in our database search which did not include 'climate change' as a search term.

The number of range shifting species is a conservative estimate due to our strict criteria for inclusion and issues of data availability and quality. Our ability to track shifts was limited by the lack of published range baselines, studies that spanned the entire geographic ranges of species, and basic methodological information on sampling date and site. Additional shifts are probably documented in the grey literature and studies where shifting

species were either considered introduced species or were not the main subject of the paper. The potential for underestimation of the range shifts of marine species is revealed by the example of three common sponges along the north-eastern coast of the United States. Thoroughly exploring the coast from New Brunswick, Canada, to New York, in the 1940s and 1950s, Hartman failed to find three species, *Halichondria bowerbanki*, *Haliclona canaliculata* and *Chalinula* (formerly *Haliclona*) *loosanoffi* north of Cape Cod, MA (Hartman, 1958). Over the past 50 years, all three have been recorded as far north as Maine and Canada, yet without literature comment as to their expansion.

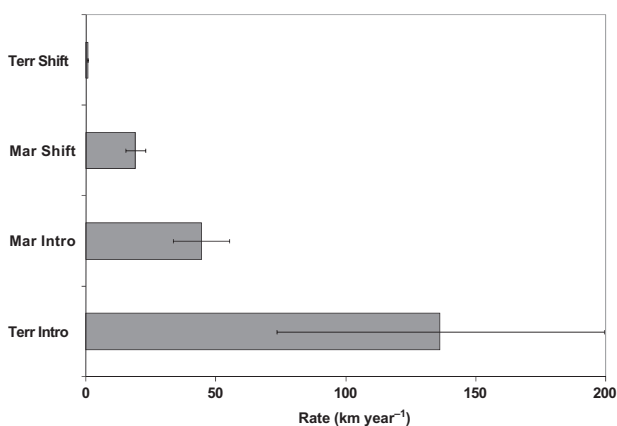


Figure 2 Comparison of spread rates of range shifts (Shift) to introductions (Intro) of marine (Mar) and terrestrial (Terr) species. Number of species represented and sources are: terrestrial shifts ($n = 99$; Parmesan & Yohe, 2003), marine shifts ($n = 73$; this study), marine ($n = 26$) and terrestrial introductions ($n = 13$) (Grosholz, 1996; Kinlan & Hastings, 2005). See Table 1 and Appendices S1 and S2 for more information on the species represented. Data are means \pm 1 SE.

Range shifts occurred much faster in marine systems than terrestrial systems (see also Mieszkowska *et al.*, 2005). This result is congruous with the common assumption that marine populations are more open than terrestrial populations (Caley *et al.*, 1996). However, the majority of the species considered in our analysis disperse quite locally (e.g. many of the seaweeds; see Gaylord *et al.*, 2002, and Kinlan & Gaines, 2003), but they still spread more rapidly than the primarily mobile species shifting in terrestrial systems (Parmesan & Yohe, 2003).

Rates of marine range shifts are an order of magnitude higher than predicted rates of shifts in global surface temperature clines. For example, species living at temperate latitudes are predicted in general to shift by $0.74 \text{ km year}^{-1}$ in response to temperature increase, based on a constant temperature increase of $0.0074 \text{ }^{\circ}\text{C year}^{-1}$ over the last century (IPCC, 2007a) and a rough isotherm relationship of $100 \text{ km} = 1 \text{ }^{\circ}\text{C}$ (Hughes, 2000). Although this predicted rate closely approximates that of terrestrial shifts ($0.61 \pm 0.24 \text{ km year}^{-1}$), the deviation from the rate of marine shifts is striking, especially given that many of the marine species are intertidal and would be expected to respond to both immersed and emersed temperature changes (see Wethey & Woodin, 2008). It is likely that these calculations are less representative of marine conditions, as they are predicted mean global temperature changes, and regional temperature changes vary greatly. Hansen *et al.* (2006) found that sea surface temperature isotherms shifted between 3 and 6 km year^{-1} in Europe between 1975 and 2005, values that come closer to the mean rate of range shifts found in our study. Although the nine polar (found at $> 60^{\circ}$ latitude) species and species groups shifted faster than average ($28.0 \pm 17.9 \text{ km year}^{-1}$) – congruent with the observation and prediction that polar regions are warming faster than temperate regions (IPCC, 2007a) – removing these species only decreases the overall spread rate by about 1 km

year^{-1} . It may be that the ranges of marine species are limited by another aspect of temperature (e.g. maximum or minimum, extremes or seasonal patterns), another climate variable or species interactions (see Harley *et al.*, 2006; Helmuth *et al.*, 2006). Clearly, better predictors of rates of marine range shifts are needed, as well as a better understanding of dispersal rates of marine organisms (Kinlan & Gaines, 2003; Byers & Pringle, 2006; Dunstan & Bax, 2007).

The difference in spread rates of marine species, with introductions occurring over twice as fast as range shifts, may be indicative of the ecological differences between these two processes as postulated in the Introduction. Introductions may be faster due to predatory or competitive release and prey naïvety in the recipient community (Blossey & Nötzold, 1995; Colautti *et al.*, 2004; Salo *et al.*, 2007). Any advantages that range shifters might have in being better matched to the habitat and having higher propagule pressure from local source populations are not apparent. The rate difference also does not seem to be explained by the taxonomic representation, which was similar between the two groups (Appendix S2). Alternatively, we acknowledge that the introduction spread rates may be inflated by cases of continued anthropogenic transport that we were not able to detect and remove from the analyses. Thus, it seems likely that we have over-estimated, rather than under-estimated, the difference in range shift and introduction spread rates.

Predicting spread rates in more than a general sense will be difficult, even for repeated introductions of some of the best-studied introduced species (Lyons & Scheibling, 2009). For example, predicted spread rates of the green crab *Carcinus maenas* on the North American east coast and in South Africa had errors of 32–130% when based on data gathered in California (USA) (Grosholz, 1996). In addition, a spread-rate model created for *C. maenas* was no better at predicting subsequent introductions of the same species than it was at predicting the spread of a suite of marine and terrestrial species (Grosholz, 1996). Thresher *et al.* (2003) continued the analysis of *C. maenas* introduction dynamics and suggested that, despite its planktonic larval stage, recruitment is typically localized, with occasional long-distance dispersal events. Similarly, Duncan *et al.* (2009) invoke differences in climatic, biotic and dispersal variables to explain the inability of climate envelope models based on native ranges of dung beetles (in South Africa) to predict introduction dynamics in Australia.

Although introduced species spread faster than range shifters, this result did not correspond to greater impacts of introduced species in the recipient communities; range shift effects were of the same or higher magnitudes than introduction effects for four out of five of the ecological effect categories (Fig. 3). Shifting species can have negative effects on the recipient communities, and thus can be termed ‘invasive’ as applied to introduced species that have negative ecological or economic effects. The magnitudes of shifters’ effects could be amplified or diminished by cascading and indirect effects (e.g. Hogg & Morton, 1983; Zimmerman *et al.*, 1996; Hollebone & Hay, 2008) or by interactions among multiple synchronous shifts (Piazzi & Cinelli, 2003; Rivadeneira & Fernández, 2005). The information gap on

Table 2 Marine species undergoing range shifts that have had documented community and ecosystem effects.

Ecological effect	Taxon	Species	Specific effect	Effect size	Reference
Disease	Protist	<i>Perkinsus marinus</i>	Decreased oyster survival	-0.24	Ford & Smolowitz (2007)
Competition	Seaweed	<i>Fucus serratus</i>	Decreased 2 seaweeds' cover	-1.14	Arrontes (2002)
Herbivory	Gastropod	<i>Patella ulyssiponensis</i>	Decreased seaweed cover	-0.19	O'Connor & Crowe (2005)
	Gastropod	' <i>Lottia</i> ' <i>depicta</i>	Decreased seagrass growth	-0.28	Jorgensen <i>et al.</i> (2007)
	Gastropod	' <i>Lottia</i> ' <i>depicta</i>	Decreased seagrass biomass	-0.66	Zimmerman <i>et al.</i> (1996)
	Crab	<i>Petrolisthes armatus</i>	Decreased microalgal biomass	-0.14	Hollebone & Hay (2008)
Predation	Urchin	<i>Centrostephanus rogersii</i>	Decreased seaweed biomass	-8.35	Ling (2008)
	Squid	<i>Dosidicus gigas</i>	Decreased fish (hake) abundance	-1.03	Zeidberg & Robison (2007)
Nutrients	Bird	<i>Larus delawarensis</i>	Increased local nitrate	2.06	Hogg & Morton (1983)
	Bird	<i>Larus delawarensis</i>	Increased local phosphorus	3.78	Hogg & Morton (1983)
	Bird	<i>Larus delawarensis</i>	Increased cover of introduced plants	2.29	Hogg & Morton (1983)

See Appendix S5 for references.

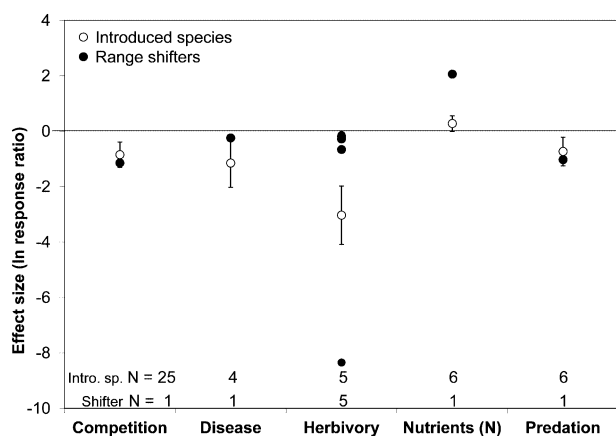


Figure 3 Effect sizes (ln-transformed response ratios) of impacts of shifting (filled circles) and introduced species (open circles) on recipient communities. Introduced species values are means \pm 95% bootstrap CI for $n = 25$ (competition), 4 (disease), 5 (herbivory), 6 (nutrients; nitrogen) and 6 (predation) studies. Each filled circle represents the effect size from a single species in a single study (shifting species herbivory values represent four species, including the values of two studies for one particular species; all five values are averaged for the analyses).

multiple range shifts also exists for multiple introductions (Grosholz, 2005; Williams, 2007; Williams & Grosholz, 2008). Recent studies have highlighted the importance of incorporating knowledge of species interactions when making predictions of effects and the limitations of climate envelope techniques in predicting establishment and spread (Helmuth *et al.*, 2006; Sax *et al.*, 2007). Accurate prediction of range shift rates and effects requires a wealth of information about range-limiting factors in the native community, environmental tolerances and species interactions (Harley *et al.*, 2006; Helmuth *et al.*, 2006; Kearney & Porter, 2009), and similar data are necessary for introductions (Kolar & Lodge, 2001; Herborg *et al.*, 2007; Schaffelke & Hewitt, 2007). To this end, risk assessment methodology being developed for introduced species might transfer nicely to better

predict the effects of climate-driven range shifts (Lodge *et al.*, 2006; Williams & Grosholz, 2008).

Characteristics of shifting species and range shift-prone locations

Successful shifting species share traits documented and hypothesized for successful introduced species, such as competitive and predatory superiority, life histories with short generation times and broad environmental tolerances (see summaries in Lodge, 1993; Rejmánek & Richardson, 1996; Vermeij, 1996, and Kolar & Lodge, 2001). For example, the shifting alga *Fucus serratus* has higher reproductive output, survival and growth rates than the native competitor *Fucus vesiculosus*, which it suppresses (Arrontes, 2002). Perry *et al.* (2005) found that shifting fish species tended to have smaller body sizes, faster maturation and smaller sizes at maturity than species with stable range boundaries. Rivadeneira & Fernández (2005) reported a positive relationship between spread rate and the proportion of microhabitats occupied by 10 shifting intertidal species. They suggested that specialists and generalists are more prone to contractions and expansions, respectively.

Although there is a commonality in traits of successful shifting and introduced species, one interesting difference was found. Distinctiveness in the community has been associated with introduction success (Strauss *et al.*, 2006b). For example, the introduced snail *Littorina littorea* has no ecological analogue of similar body size and has become the dominant snail grazer along much of the east coast of North America (Bertness, 1984). Distinctiveness – and lack of defences – could help to explain the greater impact of introduced pathogens than the shifting oyster protistan parasite. However, at least six examples of shifting species that affect the recipient community *did* have a local ecological analogue. These analogues were either congeners (e.g. of *Larus delawarensis* and *Patella ulyssiponensis*) or functionally similar (e.g. oyster parasites in addition to *Perkinsus marinus* and 'commensal' limpets in addition to '*Lottia*' *depicta*). In all cases, these analogues were present in lower densities or were less conspicuous than the shifting species (e.g. Hogg & Morton,

1983; Zimmerman *et al.*, 1996; O'Connor & Crowe, 2005). Future studies should focus on determining which shifting species are likely to have the greatest impacts, with keystone and habitat-forming species being likely candidates (Sanford, 1999; Helmuth *et al.*, 2006; see Williams & Grosholz, 2008, for similar recommendations for introduced species). For example, we found that the sea urchin *Centrostephanus rodgersii* had the strongest community impacts; it would also most probably be termed a 'keystone' species among the eight species with documented ecological effects.

There were few range shift studies that addressed how characteristics of recipient communities, as opposed to species traits, allowed the establishment of range shifting species; however, some interesting community patterns are apparent. As for introductions (Ruiz *et al.*, 1999; Williams, 2007; Williams & Smith, 2007), we found examples of shifters spreading into areas with higher levels of disturbance, predatory release, competitive release and prey density (Lodge, 1993; Vermeij, 1996; Colautti *et al.*, 2004). Arrontes (2002) found that *Fucus serratus* shifted faster into disturbed areas. The barnacle *Tetraclita rubescens* is an example of a shifting species that experiences predatory release (Sanford & Swezey, 2008). In laboratory experiments, *T. rubescens* suffered 62% mortality due to a predatory whelk from its native range but no mortality from a predatory whelk in the expanded portion of its range. Competitive release may have allowed range shifts to occur in locations with abundant prey where functionally similar species were present in low densities (such as seagrass for the limpet '*Lottia*' *depicta* and oysters for the parasite *Perkinsus marinus*), which is analogous to the relationship of higher invasibility by non-natives where resources are abundant (Vermeij, 1996). However, some species shifted where available resources were not apparent, such as the limpet *Patella ulyssiponensis*, which shifted into a habitat containing a suite of native and non-native competitors (O'Connor & Crowe, 2005).

CONCLUSIONS AND FUTURE DIRECTIONS

We have collated studies demonstrating that shifts in the ranges of many marine taxa, not just their relative abundances, have occurred, as observed on land and ascribed to climate change. Community impacts of these shifts, although of similar magnitudes to those of introductions, have been documented for fewer than 10% of shifting species. Over a hundred documented marine range shifts exist providing opportunities for scientists to address their consequences. These range shifters almost certainly represent only a fraction of the marine and estuarine species that have moved or are now on the move; large distributional data sets such as the Continuous Plankton Records are a promising place to start comparing current and historical ranges (Barnard *et al.*, 2004; Hays *et al.*, 2005). Additional species are likely to be poised for future range shifts, such as North Pacific Ocean species for which continued climate warming may allow migration through Arctic corridors into the North Atlantic Ocean (Reid *et al.*, 2007; Vermeij & Roonpurne, 2008), as occurred during earlier

Tertiary episodes (Vermeij, 2005). This opportunity for migration was afforded by the opening of the Northwest Passage during the summers of 2007–2009 (http://www.esa.int/esaCP/SEMYTC13J6F_index_0.html). Finally, there exists a third category of climate change-driven range shifts that begs future study: the neo-expansion, or resumed expansion, of non-native species that long ago spread and established range boundaries at their thermal limits (Carlton, 2000). Such studies are limited by few data and the difficulty of pinpointing the spread timeline and drivers; however, they would allow us to determine whether spread rates and community impacts of neo-expanding introduced species are more similar to those of native range shifters or introduced species undergoing their initial expansion.

Although marine species undergoing range shifts are likely to spread more slowly than marine introduced species, their community-level effects could be as great, and in the same direction, as those for introduced species. Thus, just like introductions, range shifts have the potential to seriously affect biological systems. The potential for disruption has been largely overlooked in range shift studies, which have been focused primarily on whether native species can shift their ranges or evolutionarily adapt fast enough to keep pace with changing climate. This focus has stemmed from a concern that climate change will lead to extinctions and the loss of biological diversity, which has resulted in proposals for 'assisted colonization' or the deliberate movement of species to mitigate biodiversity loss (Hoegh-Guldberg *et al.*, 2009). Our review provides evidence that the concern for biodiversity and community function (Ricciardi & Simberloff, 2009) transcends whether species can keep pace with climate change given that shifting species could begin to function as invasives and perturb recipient communities. In addition, marine communities might be affected more quickly than terrestrial ones as species shift with climate change, given that rates of range shifts are faster in marine than terrestrial environments. Regardless of habitat, consideration of range shifts in the context of invasion biology can improve our understanding of what to expect from climate change-driven shifts as well as provide tools for formal assessment of risks to community structure and function.

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SUPPORTING INFORMATION

Additional Supporting Information may be found in the online version of this article:

Appendix S1 Species included in marine introduction rate comparison.

Appendix S2 Taxa represented in spread rate calculations.

Appendix S3 Impacts studies of introduced non-native species.

Appendix S4 Supplementary materials and methods.

Appendix S5 References for studies used in the meta-analyses.

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BIOSKETCHES

Cascade Sorte studies the effects of global change on marine systems and, in particular, how climate change will modify the impacts of introduced species. Cascade aims to predict community responses to ocean warming by integrating ecophysiological studies of single species, field observations, community temperature-increase experiments and simulation modelling.

Susan Williams is a nearshore and estuarine benthic ecologist with broad interests in the maintenance of biodiversity at all levels and its importance for ecosystem function. She is President (2009–2011) of the Coastal and Estuarine Research Federation.

James Carlton's research focuses on the environmental history of near-shore marine communities over the past several millennia, particularly additions (human-mediated invasions, including their ecology, biogeography and management) and deletions (both human-mediated and natural extinctions). Jim is also the editor of the *Intertidal Invertebrates from Central California to Oregon*.

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