

Chapter 14

Competition in Marine Invasions

James E. Byers

14.1 Introduction

Competition is a negative interaction between two or more species that utilize the same shared, limiting resource (Connell 1983). Although competition can have large local, immediate effects, (e.g. on demography, resource use, etc.), competition in many marine systems is often assumed to have minimal effect on population persistence, primarily due to characteristics of the dominant life histories of marine organisms. Notably, a large proportion of marine species have pelagic larvae and thus often reside in open populations where the supply of progeny is decoupled from progeny production. Thus, although competition can still affect adults, future generations are supplied from distant populations that can “rescue” populations of inferior competitors from being excluded. Even in relatively closed marine habitats, e.g., bays or estuaries, a constant influx of larvae in ballast water (Verling et al. 2005) may make many populations effectively open, subsidizing populations of species that would otherwise be excluded. The open nature of larval production and delivery applies to food resources as well. The preponderance of filter feeders, which feed on a food resource that is typically replenished frequently (e.g., with tidal cycle) and whose supply is often decoupled from consumptive pressure by resident organisms, may reduce the occurrence of resource competition.

Bringing evidence to bear on the frequency and strength of competition in marine species is not easy. Experimental manipulations are usually logistically difficult. For example, planktonic species are extremely hard to track because of their small size and fluidity. Also, dramatic ontogenetic changes and concomitant dietary and habitat shifts are common as well, meaning that even if competition between some life stages can be elucidated, its relative importance on populations overall may be difficult to assess. Thus, particularly in marine systems where logistical and common life history characteristics can make competition hard to study, it is important to assess what has been done, how well it has been done, and what future research needs are.

To illuminate the larger issues regarding the commonality of competition in marine invasion, how central a role it plays, and biases in its study, I reviewed the

marine literature. I used the resulting database to address not only how often competition with exotic species significantly affects native species, but also the responses typically measured to index competitive effects, the taxa commonly studied for competitive interactions, and the marine habitats and regions represented. Furthermore, I examined the database to see whether some characteristics of marine lifestyles (e.g., open systems, filter feeding) mitigate competition's role in marine invasions.

14.2 A Review of the Competition Literature on Marine Invasive Species

I searched the peer-reviewed literature in ISI Web of Science (covering 1977 through June 2005) and Aquatic Sciences and Fisheries Abstracts (covering 1971–June 2005). I used the search terms: (marsh or estuar* or bay or sea or coast* or marine or ocean*) and compet* and (inva* or introduc* or alien or nonnative or non-indigenous or non-native or non-indigenous). Such a broad, inclusive search allowed even studies that only mentioned “competition” (or any root of the word) to be examined. Initial searches produced nearly 300 papers on competition in marine invasions. Several studies on anadromous fish, e.g. salmon, were excluded because all the competition work was done in freshwater habitats and life stages. Articles were indexed according to the nonindigenous species examined, habitat, feeding mode, geographic location of the study, response variables measured, whether appreciable competition was concluded by the study, and what type of evidence was brought to bear on this conclusion. The evidence comprising this latter category was classified as one of five types: experimental; natural experiment or sampling of natural pattern; component parts demonstrated (e.g., dietary overlap or resource conversion efficiency relative to a similar native species); correlational or observational measures; or assumed or stated as background information (often by relying on previous studies). Studies in the last category were excluded from the database; however, the original sources upon which these studies often relied were usually already contained in the database.¹

¹ Although these evidence categories somewhat reflect the strength of the evidence for competitive interactions, there can be exceptions. For example, although papers under the category “competition assumed” were excluded from analyses, the category of course does not necessarily indicate that the inference of competition is incorrect. An exotic species that forms a dense monospecific stand soon after invading is often presumed to be a superior competitor. Common examples in the literature include *Mytilus galloprovincialis*, *Spartina* sp., and *Caulerpa taxifolia* where researchers cite the fast dominance and loss of similar native species as evidence of competition. For some species, such a conclusion may be well accepted without much direct experimental evidence. Nonetheless, experimental documentation is still the gold standard for competition since negative covariation in native and exotic species' abundance can also be driven by underlying environmental factors, like climate shifts, disturbance, etc. Experiments explicitly document the mechanisms of interaction and success.

To enhance the independence of the database, multiple studies by the same lead author on the same species were only counted once. Specifically, I included the study that used the most rigorous approach to examine the presence of competition. Careful review of all papers yielded 80 that met the described criteria and these were analyzed for three primary aspects. First, to examine the frequency with which various nonindigenous taxa were studied for competition, each nonindigenous species in each competition study was counted. That is, if multiple exotic species were examined within a single study, each species was tallied. Then, to determine how broadly a given taxonomic group had been studied, I next tallied the occurrence of nonindigenous species in the database only once, regardless of how many times it was studied. Second, to understand where marine invader competition studies were conducted, I recorded the geographical regions of each study; such a *per study* basis avoided over-weighting studies that had examined multiple species.² I also tallied the marine habitats examined in the studies, counting each habitat only once per species, thus avoiding multiple counts of habitats that re-occurred for commonly studied species. Third, I calculated the overall frequency of competition on a *per study* basis.

14.2.1 What Exotic Taxa are Studied for Competitive Interactions?

The top two taxonomic groups studied for competitive effects were molluscs and algae, which accounted for greater than 60% of all studies in the database (Fig. 14.1). After adding the tunicates, arthropods (represented almost exclusively by crabs), and marsh grasses to this assemblage, these top five taxonomic groups comprised nearly 90% of all competition studies on nonindigenous species. Again, these numbers are conservative because they exclude multiple studies done by a lead author on the same species.

Because competitive interactions of several nonindigenous species were examined in multiple studies, an alternative way of examining the database is to look at how many distinct nonindigenous species are represented in each taxonomic group. This approach counts each species only once, irrespective of how often it may have been examined by multiple studies. In other words, it addresses whether a well-studied taxonomic group in the previous analysis (Fig. 14.1a) is composed of a few studies on many species, or many studies on a few species. For the most part, the greater the number of studies, the greater the number of nonindigenous species represented in a taxonomic group (Fig. 14.1). Thus, the relative rankings of the taxonomic groups was essentially unchanged from the previous analysis with the

²Berman et al. (1992) was treated as three separate studies because it compared and contrasted patterns of three very distinct invaders that drew upon independent datasets and approaches to evaluate each species.

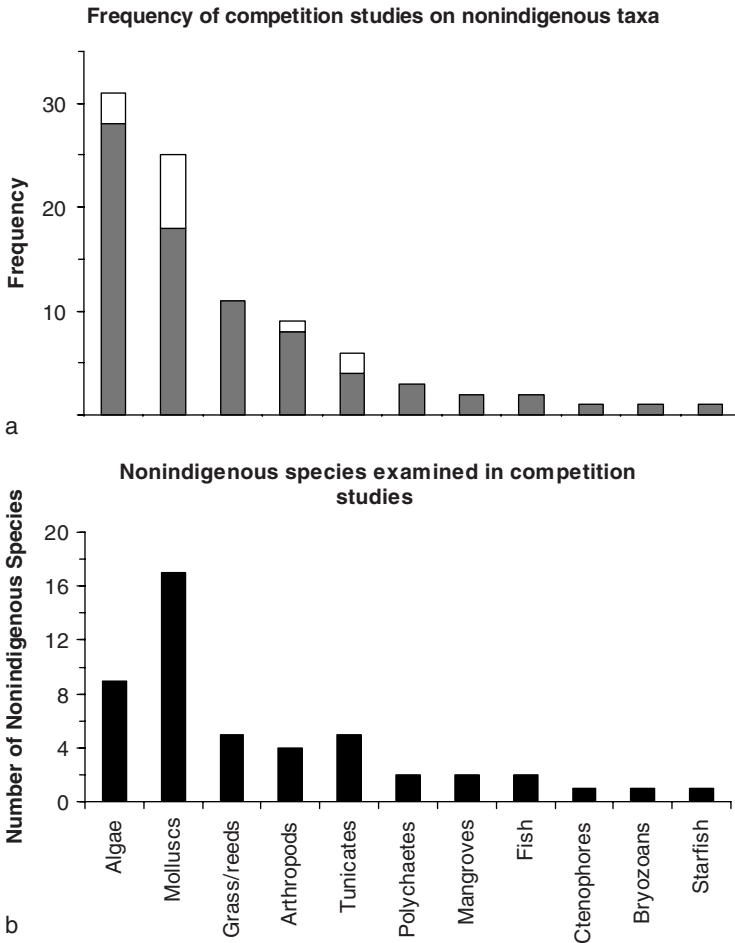


Fig. 14.1 Total number of competition studies (by distinct first authors) on nonindigenous marine species categorized by taxonomic group. Four studies examined competition between exotic species; however, the grand majority examined effects of one or more exotic species on one or more native species. If multiple nonindigenous species were examined in a single study, each species was tallied. **a** *Open white bars* represent competition studies where no competition was detected with a native species; *solid bars* represent competition studies where competition was concluded to be occurring. **b** Number of different nonindigenous species examined for competition within each taxonomic group. This figure reflects how many different species are represented in the competition studies depicted in **a**

notable exception of molluscs surpassing algae as the most broadly studied group (Fig. 14.1b). That is, molluscs are represented by many species with a few studies each, compared to algal species, which are represented by many studies on a few species. As a case in point, the algae *Caulerpa taxifolia* and *Sargassum muticum* had 9 and 10 competition studies, respectively, accounting for >60% of all exotic algal competition studies. In total, 49 exotic marine species have been studied for competitive effects (and only 26 have been studied experimentally), with molluscs and algae representing >50% of these.

14.2.2 What Regions and Habitats are Studied?

Geographically, 83% (66/80) of the marine invader competition studies were conducted in Europe and North America. Even here the effort was not even, because almost all of studies in North America come from the northeastern United States and the US Pacific coast. Of the sole nine studies from the southern hemisphere, four were from Australia and three from South Africa (and all three focused on the same species—*Mytilus galloprovincialis*, see Chap. 24, Hayden et al.). Although some of the nonindigenous species studied for competition were tropical in origin (e.g., *Caulerpa taxifolia*), only three competition studies on exotic species have been performed in the tropics—two in Hawaii (Zabin and Hadfield 2002; Krauss and Allen 2003) and one in Guam (Braley 1984). This lack of competitive studies may be partially attributable to a paucity of invaders in the tropics or because we have only sparse data on the extent of marine invasions in the tropics (e.g., Coles et al. 1999; Englund 2002).

All studies were conducted near shore. However, author-defined habitats indicated a reasonably even spread of studies throughout nearshore habitats (Fig. 14.2). Studies were not exclusively confined to sheltered habitats that might at least superficially seem to offer more tractable study conditions. About half of the competition studies were performed on coasts, seas, or fjords/sounds. Very few studies were explicitly subtidal (e.g., Britton-Simmons 2004; Ross et al. 2004). The few studies that concluded no significant competition was occurring were spread fairly proportionately throughout the habitat types.

14.2.3 How Often Does Competition Occur and How Are Its Effects Measured/Indexed?

Initial searches produced nearly 300 papers on competition in marine invasions. However, more than two-thirds of these were excluded because they only assumed competition, or stated it as background information by relying on previous studies. Most of the studies where competition was assumed were for species that were not necessarily more difficult to measure or manipulate. Several were

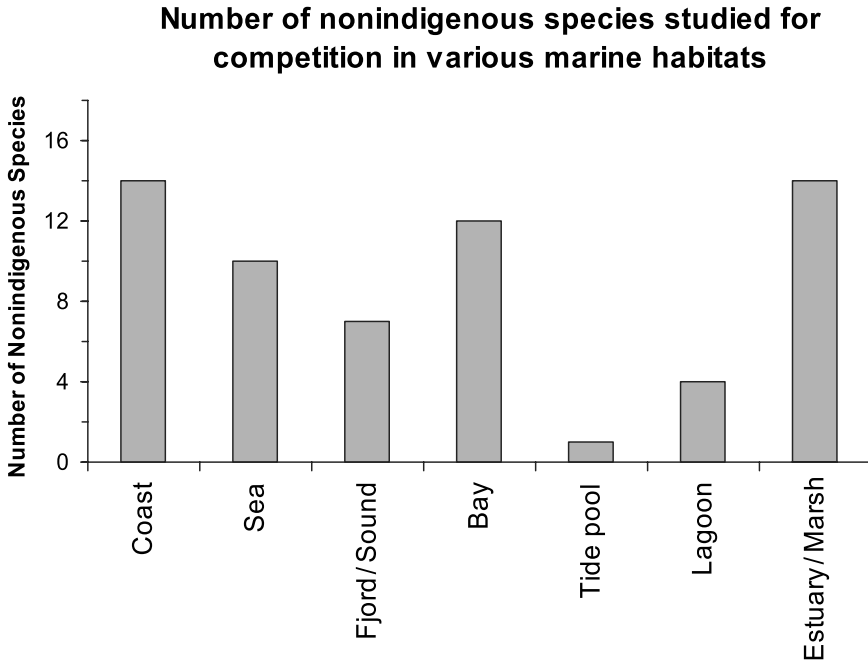


Fig. 14.2 The number of nonindigenous species studied for competition in various marine habitats. These habitats have overlapping definitions, but I used the authors' designations as best I could. The graph is based on the number of distinct species instead of studies to avoid taxonomic inflation that could result from having multiple studies of the same species in the same habitat type. However, this analysis is not completely independent of taxonomy since some species were studied in more than one habitat, e.g. oysters, and were counted for each of those habitat types. Habitats are subjectively ranked in order of openness from most to least. (Although tide pools are extremely closed habitats at low tide, this is offset by their connectedness to the larger adjacent habitat at high tide)

species that authors cited had been already documented in other studies as highly competitive (e.g. *Caulerpa taxifolia*, *Mytilus galloprovincialis*). Many others (e.g., Pipitone et al. 2001) were largely descriptive studies merely suggesting reasons for an invader's success.

Of the studies in the database where competition was directly addressed, 80% (64 of 80) concluded significant competition between exotic and native species was occurring, in some cases with dramatic effects like local exclusion. Five of these studies concluded that competition was occurring only with some studied native species, while other native species in the study were not affected. For example, Crooks (2001) showed that byssal mats formed by the Asian mussel *Musculista senhousia*, significantly affected growth and survivorship of the surface dwelling, suspension feeding clam, *Clione* sp., while the deep dwelling deposit feeding clam, *Macoma nasuta*, was unaffected (see Chap. 18, Hewitt et al.). Four additional

studies in the database (5%) did not involve native species and examined competition between two exotic species (Piazzini and Cinelli 2001; Piazzini and Ceccherelli 2002; Krauss and Allen 2003; Ross et al. 2004); significant competition was concluded in all four.

Of studies in the database, 15% concluded that no appreciable competition between nonindigenous species and native species was occurring. This percentage was essentially identical (16%) if just looking at studies where competition was experimentally examined ($n=37$). These studies that found no significant competition were spread fairly proportionately throughout the habitat types. I explored the 12 studies on 13 species that found no competition to determine if there were any unifying characteristics. Of the 13 studied species, 10 were animals, 8 of which were filter feeders (6 molluscs and 2 tunicates). Filter feeders have been proposed to experience reduced competition because the planktonic food resource on which they feed is often not a limiting factor (Levinton 1972; Peterson 1979; Byers 2005). Especially in areas with appropriate tidal flushing, food can replenish quickly. However, despite the expectation that filter feeders may have one less resource for which to compete, reducing the overall likelihood or magnitude of competition, filter feeders were not overly represented in the “no competition” subset of studies relative to their overall frequency in the database.

Typical of competition studies in general, growth, fecundity, survivorship, and avoidance behavior were commonly recorded response metrics. Many studies used several of these response variables in combination. For example, Britton-Simmons (2004) in Washington USA showed that native brown and red algal species were more abundant and native kelp grew twice as fast where the Asian alga *Sargassum muticum* was experimentally removed. Complementary measurements in experimental plots identified shading as the mechanism of competitive impact on natives rather than changes to water flow, sedimentation, or nutrient availability. Also, in Washington USA Byers (2005) examined whether increasing densities of the Asian clam, *Venerupis philippinarum*, influenced growth, survivorship, and fecundity of a confamilial native clam, *Protothaca staminea*. Even at experimental densities 50% higher than any measured in field, *Venerupis* has no direct effect on itself or *Protothaca*. Differences in the clams' burial depths apparently minimized competition for space and exploitative competition between these filter feeders was minimal.

Some studies, particularly those that examined algae, showed local competitive exclusion, at least over small spatial scales. For example, in New England USA, Bertness et al. (2002) quantified the percentage of shoreline developed at the terrestrial edge of salt marshes, which strongly influenced nitrogen run-off. In turn, nitrogen availability explained 45% of the variation in the dominance of the invasive marsh reed *Phragmites australis*. Thus, nutrient enrichment associated with shoreline development gave *Phragmites* competitive advantage over traditional high-marsh vegetation. In some areas *Phragmites* expansion (coupled with native *Spartina alterniflora* expansion from the low marsh) reduced plant species richness fivefold, creating species-poor monocultures.

14.3 Should Competition be Stronger in Human Mediated Invasions?

The collective conclusion of these studies was that competition was frequent and strong. In this section I outline three key ways that humans have altered colonization events that may enhance the role of competition in invasions, especially compared to historical invasion processes, i.e., natural colonization.

First, rapid rates of human-mediated invasions are several orders of magnitude greater than natural background rates (Cohen 2005). With the accelerated pace of species invasion mediated by humans, co-evolution and competitive exclusion have little time to re-equilibrate a community after an invasion before the next invader arrives. The rapidly assembled (or amended) communities have insufficient time for co-evolution to mitigate species interactions like competition, e.g. through character displacement. At least one theoretical work that has treated natural and human mediated invasions as distinct demonstrated a difference in the way that colonization mechanisms structure communities. Rummel and Roughgarden (1985), using a Lotka-Volterra framework, compared communities with the same resource distribution that were coevolution-structured (i.e., analogous to natural, well-spaced colonization events) and invasion-structured (i.e., analogous to human-mediated, rapid introductions). Both model communities were the same except that in coevolutionary trials after every invasion the community was allowed to coevolve to a new equilibrium. The alternation of invasion and coevolution continued until further invasions were not possible or until a cycle developed. In contrast, invasion-structured communities were continually subjected to invasions with no coevolution occurring between invasions. Invasion-structured communities ended with more species and with smaller niche separation than the coevolution-structured communities. The close packing of species in invasion communities resulted in higher competition coefficients and caused invasion structured communities to be less stable. This theory could be extended to predict, for example, that the 260+ nonindigenous marine and estuarine species in San Francisco Bay may still be far from asymptoting, and the Bay may be able to attain higher species diversity in modern times full of invasive species than it did of natives historically.

Second, human mediated transport of propagules causes a breakdown of one of the key assumptions of succession theory and community development—the trade-off exhibited by each species in its colonization and competition abilities. Theory predicts, and some empirical work shows, that the best colonizers and dispersers are the weedy species, which in turn compete poorly during successional processes when the more slowly arriving, but superior competitor species displace them (e.g., Clements 1916; Huston and Smith 1987; Tilman 1990). Poor competitors survive in the system through their dispersal advantage. Humans now artificially disperse large number of species, increasing the opportunity for establishment and causing a breakdown in the classic tradeoff. A species can now be

a great competitor and have its dispersal placed on equal footing with the naturally good dispersers (but poor competitors). For example, tens of millions of metric tons (MT) of ballast water are discharged yearly into US ports, with each MT on average containing ~1,000–10,000 zooplankton organisms (Verling et al. 2005). With invasive propagule pressure (Chap. 10, Smith) now boosted enormously by humans in many places, colonization of novel environments is seldom determined by a species' own dispersal abilities. Given the magnitude of these new, human-mediated vectors, good competitors should be showing up far more frequently than they would naturally.³

Third, sharp increases in anthropogenic disturbances may alter the receptiveness of a community to colonizers (see also Chap. 7, Johnston et al.; Chap. 12, Olyarnik et al.). Specifically, such disturbances may override a previous ability of a native species to exclude invaders preemptively, thus increasing the ability of a colonizing nonindigenous species to compete its way into a community. Theoretically, one might assume that resident species should have the upper hand when competing with invasive species because the residents, with thousands of years of incumbency, should be best adapted to the local environment (Vermeij and Dudley 2000). However, environments that have been seriously altered by anthropogenic disturbance outside the magnitude, duration, or frequency of natural disturbances that affect communities, can create a mismatch between traits of the native species and the environmental conditions to which they have long adapted—a phenomenon termed selection regime modification (Byers 2002). Nonindigenous species may have equal opportunity when these environments suddenly become just as novel for the native species as they are for the exotics (Byers 2002). Invasive species should on average have enhanced establishment success and enhanced competitive impacts in these modified areas (Wasson et al. 2005; Tyrrell and Byers 2007). As anthropogenic impacts continue at unprecedented rates in nearly all ecosystems on earth (Janzen 1998; Vitousek et al. 1997), this mechanism may be increasingly influential and may also help to explain the observed strong correlation of invasions in disturbed environments (see reviews by D'Antonio et al. 1999; Dukes and Mooney 1999). Selection regime modification has certainly occurred in many nearshore marine habitats which are heavily disturbed. Salt marshes, for example, are heavily filled and channelized, and receive high quantities of freshwater runoff and contaminants (e.g., Cairnes 1993; Kennish 2001; Valiela et al. 2004) and also contain relatively large numbers of invasive species.

³Ballast subsidies not only dismantle the competition-colonization trade-off allowing strong competitors to overcome dispersal limitation and invade, but additionally, poor competitors, once arrived, can often persist artificially through the help of such human-mediated propagule subsidies.

14.4 Caveats to the Conclusion of Strong and Frequent Competition in the Marine Invasion Literature

In general reviews of competition in aquatic and terrestrial habitats (not just reviews of invasions), significant competition was also found to occur in a majority of studies that explicitly examined its presence (Connell 1983; Schoener 1983; Gurevitch et al. 1992; Bruno et al. 2005). However, due to publishing biases, where only positive results are published, or studies are conducted on species where competition is thought to be occurring, competition's common occurrence is not supported by thorough, unbiased literature. Competition studies of marine invaders share this general bias. Additionally, inventories of nonindigenous species (which thus dictate the candidate species for nonindigenous competition studies) are themselves biased because of historical records and modern sampling efforts that favor detection of exotic species that are larger and are economically or culturally important (Ruiz et al. 2000; Byers, in press). Furthermore, competition studies on marine invaders do not draw proportionately from the biased nonindigenous species inventories and are themselves skewed further toward larger, conspicuous, easily-accessed taxa. Given the young age of invasion biology as a discipline and the field's relevance to applied issues, it is perhaps unsurprising that published studies focus on species that are abundant, problematic, conspicuous, and easy to access.

On the positive side, molluscs and algae are the second and forth most documented exotic taxa, respectfully, in coastal North America (Ruiz et al. 2000). Twelve species (18%) of molluscs and four species of algae (16.7%) identified as established nonindigenous species by Ruiz et al. (2000) have been studied for competition.⁴ Tunicates are also well represented in competition studies with four species examined (21% of the list of Ruiz et al. 2000). However, for all other exotic taxonomic groups in North America, fewer than 10% of the species comprising them have been studied for competitive effects. The most troublesome discrepancy is with the crustaceans, which despite being the largest taxonomic group of nonindigenous species in North America (85 established exotics), has had only 3 species (~3.5%) studied for competitive effects. Annelids are the third largest nonindigenous group in North America (28 species), with one of these species having been studied for competition elsewhere in the world where it is also nonindigenous. The skew in studied taxa may be especially important to overall generalizations about competition gleaned from the literature because certain life history characteristics that may influence competition (e.g., brooder vs broadcast spawner; filter vs deposit feeder) are often phylogenetically correlated.

⁴One of the four algal species, *Caulerpa taxifolia*, had not invaded North America at the time of the compendium of Ruiz et al. (2000). It was included in this tally because of its subsequent high profile invasion of southern California. For molluscs, *Ovatella myosotis* was included; it is a known invader of US West coast (Berman and Carlton 1991), but in bays other than those compiled by Ruiz et al. (2000). Also, three molluscs included in this count are nonindigenous to North America, but were studied for competition elsewhere in the world where they are also nonindigenous.

The geographic skew is also particularly acute, with almost all studies carried out in temperate regions of the Northern Hemisphere; however, this is certainly where most invaders have been inventoried and studied in general. It is encouraging that species were not all studied in the most self-enclosed/confined habitats (e.g., marshes, lagoons) (Fig. 14.2); however they do almost exclusively favor the most tractable life stages (e.g., benthic adults). Finally, certain species, e.g., *Mytilus galloprovincialis*, but especially *Sargassum muticum* and *Caulerpa taxifolia*, become focal points of competition research because of real or perceived impacts on native species.

Only a handful of studies in the database reveal competitive exclusion (e.g., Bertness et al. 2002; Steffani and Branch 2005). These studies were all done at smaller spatial scales. A paucity of experimental demonstrations of invaders driving competitive exclusion of native species was also found in larger, general literature reviews that incorporated freshwater and terrestrial habitat (Simberloff 1981; Gurevitch and Padilla 2004; Bruno et al. 2005). Most studies in the database did not last more than 1–3 years and demonstrate short-term effects on demography, behavior, or reduction in biomass. However, negative demographic effects and projections of current interaction coefficients suggest that local competitive exclusion is an expected endpoint after several decades for many of the impacted native species in these studies (e.g., Byers 2000; Sebastian et al. 2002), and evidence of actual exclusion would likely increase with an increase in studies' durations. However, future competition studies should examine exclusion explicitly because presently when species compete, but no exclusion occurs, it is difficult to discern whether the lack of competitive exclusion reflects a time lag due to the length of the process (i.e., an extinction debt – cf. Tilman et al. 1994) or species coexistence due to tighter species packing in non-coevolved communities (Rummel and Roughgarden 1985). Ironically, for several of the studies where competition was only assumed (and which were therefore not included in the formally analyzed database), exclusion seems a bigger problem. This may be because competition and exclusion by certain invaders (e.g., *Caulerpa taxifolia*, *Mytilus galloprovincialis*) appear so obvious that one does not need a formal study.

Theoretically one might expect that heavy study of native-exotic competitive interactions in marshes, estuaries, and bays (Fig. 14.2) would boost the conclusion of a large role for competition overall. Populations of organisms in these semi-enclosed habitats tend to be closed and there is a high proportion of tractable, benthic species. Even planktonic species and larvae are often retained in these environments. Within closed populations competitive effects are coupled between adults and the recruiting population, making competitive exclusion likely compared to open populations where even inferior competitor species can be continuously subsidized by larval inputs from distant sources. Also because marshes in particular are often heavily altered by humans, they are a prime place for selection regime modification and thus high competitive impact by exotic species. The database however did contain a fairly wide representation of species life history attributes (e.g., broadcast spawners and direct developers) and, although many studies were in closed habitats, roughly half (36/80) were done in relatively open marine

habitats (Fig. 14.2). Also, competition was still commonly found in these open habitats perhaps because populations there can still be closed, and most importantly because many competition studies examine immediate effects of demography, fecundity, behavior, and population trends of current residents independent of recruitment (i.e., many studies did not look at long-term persistence of populations). I suspect that with more competition studies, less publication bias for positive results, and more emphasis on population level responses, enclosed habitats would have disproportionately higher incidence of competitively influential exotic species.

Although open populations of broadcast spawning organisms were represented in the database, there were still no studies in the open ocean, and few from subtidal habitats. This representation of habitats in the competition literature, although skewed, essentially reflects that few exotic species have been documented offshore (although admittedly this area is seldom examined in most nonindigenous species surveys) (e.g., Ruiz et al. 1997; Cohen and Carlton 1998; Hewitt et al. 1999). A strong habitat focus on marshes, estuaries, and bays may be appropriate since it seems that exotic marine species are more abundant in these habitats (Ruiz et al. 1997; Chap. 33, Preisler et al.). Wasson et al. (2005) documented 527 invertebrates in Elkhorn Slough, CA – 444 natives, 58 exotics, and 25 cryptogens (11% exotics). The surrounding rocky intertidal open coast contained 588 species – 567 natives, 8 exotics, and 13 cryptogens (1% exotics). Exotic species in the estuary were not only more diverse, but also more abundant than on the open coast. Byers and Pringle (2006) demonstrate that the advection typical of open coastlines make retention and thus establishment difficult and may be largely responsible for the dearth of invasive species there. If so, the very factor—a retentive environment—that likely makes population-level competitive effects more common in semi-enclosed habitats, may also be responsible for increased exotic establishment there.

14.5 Future Directions

Rather than studies which single out individual biotic mechanisms like competition, perhaps the greatest need is studies that examine the relative importance of various biotic interactions enabling invasion and governing post-invasion interactions (Bruno et al. 2005). Apparent competition in particular is one such biotic interaction whose importance is increasingly recognized in exotic-native interactions that should be considered among the typical biotic interactions like competition, predation, and facilitation. Apparent competition can result when a shared parasite or predator species mediates interactions between exotic and native competitors. Two theoretical papers have demonstrated how this interaction may substantially influence exotic species success and impact (Courchamp et al. 2002; Noonburg and Byers 2005). Certainly modern biological control practitioners have recognized the potency of apparent competition, in large part explaining why host specificity screening is a vital step before introducing potential control agents. Despite the

need to examine this important interaction, a search of ISI Web of Science using the terms: “apparent competition and (non-native or introduced or nonindigenous or invasion or invader or invasive or exotic)” yielded only 64 papers—and only one of these was a marine study (Byers 2005). Although potentially more complex because more species are involved, a theoretical expectation of the importance of apparent competition and the paucity of studies suggest a ripe avenue for future research.

The literature search presented here looked primarily at the frequency with which competition was concluded. Ideally a meta-analysis of competitive interaction strengths would be very informative; however, only 26 species in the database were examined experimentally and these experiments frequently used different response variables that make quantitative comparisons difficult. Standardization of data collected, e.g., per capita interaction strength (Wootton and Emmerson 2005), would enable future generalizations and comparisons. For example, once the quantitative invasion literature is better and more evenly developed, a formal comparison of competition between native species and human-mediated invaders vs competition between species in studies not focused on invaders (e.g., Connell 1983; Schoener 1983) would be illustrative. Comparison of interaction strengths between these two groups of studies would help to address whether competition is stronger and more frequent in human-mediated invasions.

14.6 Conclusion

Competition, or its absence, is often assumed to fundamentally influence invasion success. Several key aspects of the current, human-mediated spread of exotics suggest that competitive interaction strengths between invader and resident biota should be stronger compared to historical invasions driven by colonization events of natural means and rates. The marine literature reveals that significant competition between natives and exotics is very common. However, this synopsis is couched with caution because it is not based on a large number of data-driven studies. Fewer than half the studies in the database were experimental, and the database itself excluded many dozens of studies that only assumed competition. Furthermore, empirical studies mostly address algae and molluscs in nearshore habitats in temperate North America and Europe. While competition seems important and common in marine invasions that have examined it empirically, we must be cognizant of these biases and avoid overextending conclusions of its importance. Human-mediated invasions may provide an unprecedented opportunity to examine strong competition in action; however, to truly evaluate it well, we should gauge its strength relative to other biotic interactions and abiotic factors that determine invasion success and impact.

Acknowledgements I thank Irit Altman, April Blakeslee, Tyra Byers, John Meyer, Gil Rilov, and two anonymous reviewers for their helpful advice and editing to shape this chapter.

References

- Berman J, Carlton JT (1991) Marine invasion processes: interactions between native and introduced marsh snails. *J Exp Mar Biol Ecol* 150:267–281
- Berman J, Harris L, Lambert W, Buttrick M, Dufresne M (1992) Recent invasions of the Gulf of Maine: three contrasting ecological histories. *Conserv Biol* 6:435–441
- Bertness MD, Ewanchuk PJ, Silliman BR (2002) Anthropogenic modification of New England salt marsh landscapes. *Proc Natl Acad Sci U S A* 99:1395–1398
- Braley RD (1984) Mariculture potential of introduced oysters *Saccostrea cucullata* tuberculata and *Crassostrea echinata*, and a histological study of reproduction of *Crassostrea echinata*. *Aust J Mar Freshwater Res* 35:129–141
- Britton-Simmons KH (2004) Direct and indirect effects of the introduced alga *Sargassum muticum* on benthic, subtidal communities of Washington State, USA. *Mar Ecol Prog Ser* 277:61–78
- Bruno JE, Fridley JD, Bromberg KD, Bertness MD (2005) Insights into biotic interactions from studies of species invasions. In: Sax DF, Stachowicz JJ, Gaines SD (eds) *Species invasions: insights into ecology, evolution, and biogeography*. Sinauer, Sunderland, MA, p 495
- Byers JE (2000) Competition between two estuarine snails: Implications for invasions of exotic species. *Ecology* 81:1225–1239
- Byers JE (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. *Oikos* 97:449–458
- Byers JE (2005) Marine reserves enhance abundance but not competitive impacts of a harvested nonindigenous species. *Ecology* 86:487–500
- Byers JE (in press) Invasive animals in marshes: biological agents of change. In: Silliman BR, Bertness MD, Grosholz ED (eds) *Salt marshes under global siege*. University of California Press
- Byers JE, Pringle JM (2006) Going against the flow: retention, range limits and invasions in advective environments. *Mar Ecol Prog Ser* 313:27–41
- Cairnes J (1993) Is restoration ecology practical? *Restor Ecol* 1:3–7
- Clements FE (1916) *Plant succession*. Carnegie Institute, Washington
- Cohen AN (2005) Basis for a standard based on the natural rate of invasion. Memo to the Ballast Water Treatment Standards Committee (August 7, 2005). Appendix 5. In: Ballast water discharge standards: report and recommendation of the California Advisory Panel on ballast water performance standards
- Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. *Science* 279:555–558
- Coles SL, DeFelice RC, Eldredge LG, Carlton JT (1999) Historical and recent introductions of non-indigenous marine species into Pearl Harbor, Oahu, Hawaiian islands. *Mar Biol* 135:147–158
- Connell JH (1983) On the prevalence and relative importance of interspecific competition: evidence from field experiments. *Am Nat* 122:661–696
- Courchamp F, Langlais M, Sugihara G (2000) Rabbits killing birds: modelling the hyperpredation process. *J Anim Ecol* 69:154–164
- Crooks JA (2001) Assessing invader roles within changing ecosystems: historical and experimental perspectives on an exotic mussel in an urbanized lagoon. *Biol Invas* 3:23–36
- D'Antonio CM, Dudley TL, Mack M (1999) Disturbance and biological invasions: direct effects and feedbacks. In: Walker L (ed) *Ecosystems of disturbed ground*. Elsevier, Amsterdam, The Netherlands, pp 413–452
- Dukes JS, Mooney HA (1999) Does global change increase the success of biological invaders? *Trends Ecol Evol* 14:135–139
- Englund RA (2002) The loss of native biodiversity and continuing nonindigenous species introductions in freshwater, estuarine, and wetland communities of Pearl Harbor, Oahu, Hawaiian Islands. *Estuaries* 25:418–430
- Gurevitch J, Padilla DK (2004) Are invasive species a major cause of extinctions? *Trends Ecol Evol* 19:470–474

- Gurevitch J, Morrow LL, Wallace A, Walsh JS (1992) A meta-analysis of competition in field experiments. *Am Nat* 140:539–572
- Hewitt CL, Campbell ML, Thresher RE, Martin RB (1999) Marine biological invasion of Port Phillip Bay, Victoria. Centre for Research on Introduced Marine Pests, Hobart, Australia
- Huston M, Smith T (1987) Plant succession - life history and competition. *Am Nat* 130:168–198
- Janzen D (1998) Gardenification of wildland nature and the human footprint. *Science* 279:1312–1313
- Kennish MJ (2001) Coastal salt marsh systems in the US: a review of anthropogenic impacts. *J Coast Res* 17:731–748
- Krauss KW, Allen JA (2003) Influences of salinity and shade on seedling photosynthesis and growth of two mangrove species, *Rhizophora mangle* and *Bruguiera sexangula*, introduced to Hawaii. *Aquat Bot* 77:311–324
- Levinton J (1972) Stability and trophic structure in deposit-feeding and suspension-feeding communities. *Am Nat* 106:472–486
- Noonburg EG, Byers JE (2005) More harm than good: when invader vulnerability to predators enhances impact on native species. *Ecology* 86:2555–2560
- Peterson CH (1979) Predation, competitive exclusion, and diversity in the soft-sediment benthic communities of estuaries and lagoons. In: Livingston RJ (ed) *Ecological processes in coastal and marine systems*. Plenum, New York, pp 233–263
- Piazzi L, Ceccherelli G (2002) Effects of competition between two introduced *Caulerpa*. *Mar Ecol Prog Ser* 225:189–195
- Piazzi L, Cinelli F (2001) Distribution and dominance of two introduced turf-forming macroalgae on the coast of Tuscany, Italy, northwestern Mediterranean Sea in relation to different habitats and sedimentation. *Bot Mar* 44:509–520
- Pipitone C, Badalamenti F, Sparrow A (2001) Contribution to the knowledge of *Percnon gibbesi* (Decapoda, Grapsidae), an exotic species spreading rapidly in Sicilian waters. *Crustaceana* 74:1009–1017
- Ross DJ, Johnson CR, Hewitt CL, Ruiz GM (2004) Interaction and impacts of two introduced species on a soft-sediment marine assemblage in SE Tasmania. *Mar Biol* 144:747–756
- Ruiz GM, Carlton JT, Grosholz ED, Hines AH (1997) Global invasions of marine and estuarine habitats by non-indigenous species: mechanisms, extent, and consequences. *Am Zool* 37:621–632
- Ruiz GM, Fofonoff PW, Carlton JT, Wonham MJ, Hines AH (2000) Invasion of coastal marine communities in North America: Apparent patterns, processes, and biases. *Annu Rev Ecol Syst* 31:481–531
- Rummel JD, Roughgarden J (1985) A theory of faunal buildup for competition communities. *Evolution* 39:1009–1033
- Schoener TW (1983) Field experiments on interspecific competition. *Am Nat* 122:240–285
- Sebastian CR, Steffani CN, Branch GM (2002) Homing and movement patterns of a South African limpet *Scutellastra argenvillei* in an area invaded by an alien mussel *Mytilus galloprovincialis*. *Mar Ecol Prog Ser* 243:111–122
- Simberloff D (1981) Community effects of introduced species. In: Nitecki MH (ed) *Biotic crises in ecological and evolutionary time*. Academic Press, New York, pp 53–81
- Steffani CN, Branch GM (2005) Mechanisms and consequences of competition between an alien mussel, *Mytilus galloprovincialis*, and an indigenous limpet, *Scutellastra argenvillei*. *J Exp Mar Biol Ecol* 317:127–142
- Tilman D (1990) Constraints and tradeoffs: toward a predictive theory of competition and succession. *Oikos* 58:3–15
- Tilman D, May RM, Lehman CL, Nowak MA (1994) Habitat destruction and the extinction debt. *Nature* 371:65–66
- Tyrell MC, Byers JE (2007) Do artificial substrates favor nonindigenous fouling species over natives? *J Exp Mar Biol Ecol* 342(1):54–60
- Valiela I, Rutecki D, Fox S (2004) Salt marshes: biological controls of food webs in a diminishing environment. *J Exp Mar Biol Ecol* 300:131–159

- Verling E, Ruiz GM, Smith LD, Galil B, Miller AW, Murphy KR (2005) Supply-side invasion ecology: characterizing propagule pressure in coastal ecosystems. *Proc R Soc B* 272:1249–1256
- Vermeij GJ, Dudley R (2000) Why are there so few evolutionary transitions between aquatic and terrestrial ecosystems? *Biol J Linn Soc* 70:541–554
- Vitousek PM, Aber JD, Howarth RW, Likens GE, Matson PA, Schindler DW, Schlesinger WH, Tilman DG (1997) Human alteration of the global nitrogen cycle: sources and consequences. *Ecol Appl* 7:737–750
- Wasson K, Fenn K, Pearse JS (2005) Habitat differences in marine invasions of Central California. *Biol Invas* 7:935–948
- Wootton JT, Emmerson M (2005) Measurement of interaction strength in nature. *Annu Rev Ecol Evol Syst* 36:419–444
- Zabin C, Hadfield MG (2002) Do locals rule? Interactions between native intertidal animals and a Caribbean barnacle in Hawai'i. *Pac Sci* 56:235–236