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Fish and ships: relating dispersal frequency to success in biological invasions

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Abstract Most studies characterizing successful biological invaders emphasize those traits that help a species establish a new population. Invasions are, however, multi-phase processes with at least two phases, dispersal and introduction, that occur before establishment. Characteristics that enhance survival at any of these three phases will contribute to invasion success. Here, we synthesize information on the dispersal, introduction, and establishment of fishes mediated by ship ballast-water transport. We synthesize 54 reports of at least 31 fish species collected from ballast tanks (Phase 1), including 28 new reports from our recent studies (1986 to 1996). Our literature survey revealed 40 reports of 32 fish species whose introductions have been attributed to ballast transport (Phase 2), of which at least 24 survived to establish persistent populations (Phase 3). We detected little overlap at the species level between these two data sets (Phase 1 vs Phases 2 and 3), but patterns emerged at the family level. The Gobiidae (6 species), Clupeidae (4 species), and Gasterosteidae (1 species) were the most commonly found fish families in ballast tanks (Phase 1). The Gobiidae (13 species), Blenniidae (6 species) and Pleuronectidae (2 species) dominated the list of ballast-mediated introductions (Phase 2); gobies and blennies were the families most frequently established (Phase 3). The invasive success of gobies and blennies may be explained in part by their crevicolous nature: both groups seek refuge and lay eggs in small holes, and may take advantage of the ballast-intake holes on ship hulls. This behavior, not typically associated with invasive ability, may contribute to successful introduction and establishment by facilitating the dispersal phase of invasion. The failure of the pleuronectids to invade may reflect poor salinity match between donor and recipient regions. To develop a predictive framework of invasion success, organisms must be sampled at all three phases of the invasion process. Our comparison of two ballast sampling methods suggests that fishes have been undersampled in ballast-water studies, including our own, and that the role of ballast transport in promoting fish invasions has been underestimated.

Introduction

Human-mediated biological invasions in aquatic and marine systems are increasing in frequency around the world (Office of Technology Assessment 1993; Cohen and Carlton 1995; Ruesink et al. 1995; Carlton 1996; Ruiz et al. 1997, 1999). The success of an invader has been linked in some cases with abiotic (Moyle and Vondracek 1985; Golani 1993; Moyle and Light 1996) and biotic (Vermeij 1991; Schoener and Spiller 1995; Chapin et al. 1998) characters of the recipient community. Characteristics specific to the invader, such as genetic variability, body size, physiological tolerance, and reproductive strategy also play a role in promoting invasions (Elton 1958; Baker and Stebbins 1965; Ehrlich 1989; Lodge 1993; Rejmánek and Richardson 1996; Reichard and Hamilton 1997). However, not all successful invaders exhibit typically invasive traits. In some cases, high abundance, broad distribution, and an association with humans may increase the chances of

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successful dispersal and, therefore, invasion (Elton 1958; Lodge 1993). Given the myriad variables involved, it has, perhaps not surprisingly, been difficult to develop a general predictive framework for invasion success across taxonomic groups (Ehrlich 1986; Lodge 1993).

A clearer understanding of the invasion process may be achieved if invasions are broken down into their component phases, rather than being viewed as single processes (Carlton 1996; Vermeij 1996). These phases have been defined variously (e.g. Williamson 1996), but essentially include: (1) transport (uptake from the donor biota and transport along a dispersal pathway), (2) introduction (release or inoculation and initial survival in the new environment), and (3) establishment (survival to form a reproducing population) (Carlton 1985). A successful invader must pass through all three phases, but not all phases necessarily favor the same species' characteristics (Carlton 1996; Vermeij 1996). Further, high relative abundance, although not an invasive trait per se, will increase an invader's chance of passing through each phase. To identify traits of successful invaders, it would be best to compare the abundance and characteristics of those species that survive each introduction phase with those of species that do not survive. Where species-level comparisons among phases are particularly difficult (e.g. ballast-water transport), correspondence may be sought at higher taxonomic levels (Carlton 1985). Here, we select a particular invasion pathway, ballast-water transport in commercial vessels, and a particular taxon, fishes, to compare the family-level diversity and characteristics of species that have been dispersed, inoculated, and established.

Ballast-water transport

The largest unintentional pathway for the transport of marine organisms today is the ballast water of commercial vessels (Baltz 1991; Carlton and Geller 1993; Ruiz and Hines 1997). A typical commercial bulk vessel may carry over 30 000 metric tons (MT) of ballast water to provide stability and trim adjustment during a voyage (Smith et al. 1999). Ballast water is usually taken from the harbor in one port and subsequently may be discharged in another port (e.g. Carlton 1985; Carlton and Geller 1993; National Research Council 1996). Both ballasting and deballasting occur through openings in the ship's hull, which are covered by protective grates that only coarsely filter the incoming water. As a consequence, dense and diverse collections of organisms such as protists, diatoms, invertebrate larvae, and copepods are entrained during ballasting and survive the voyage to the next port (Medcof 1975; Carlton 1985; Hallegraeff and Bolch 1991; Baldwin 1992; Carlton and Geller 1993; Carlton 1998; Smith et al. 1999). Corrosion or occasional loss of the protective grates, or ballasting of water by gravitation (i.e. without pumps), may permit larger organisms such as postlarval fish to be ballasted (Springer and Gomon 1975; National Research Council 1996).

Ballast-mediated fish invasions

Most ballast-water surveys to date have collected few fishes (e.g. Carlton and Geller 1993; Ruiz and Hines 1997; Smith et al. 1999). It would be a mistake, however, to conclude that ballast water is an unimportant mechanism for the transfer and introduction of nonindigenous fishes. Anecdotal evidence from vessel crews and captains in USA ports indicates that fish are not uncommonly found in ballast tanks (Carlton and Geller 1993). Furthermore, for a number of known fish invasions, ballast-water transport is the only known possible vector (e.g. Carlton 1985; Miller et al. 1989; Hensley 1993).

As a taxonomic group, fishes provide a powerful tool for relating transport success to invasion success, for three reasons. First, at the transport phase, the majority of animal taxa in ballast water are often planktonic larvae of invertebrates, which are difficult or impossible to identify to species. Fishes, in contrast, are frequently collected as juveniles or adults which are more easily identified. Second, fishes are relatively large and conspicuous members of marine communities, so unusual specimens are more likely to be noted. Third, since many fish species are well described around the world, they can be classified readily as native or introduced (reviews by: Moyle 1986; Randall 1987; Pollard and Hutchings 1990; Golani 1996; Lever 1996; Fuller et al. 1999).

Herein, we synthesize information on the ballast-mediated transfer, introduction, and establishment of fishes, combining data from our own studies with published records. We determine which fish taxa occur most commonly in ballast water, and whether these occurrences correlate with suspected ballast-mediated fish invasions. While the available data do not lend themselves to rigorous hypothesis testing, we address the predictions and suggestions that ballast-water transport and invasion may be more common in crevicolous species such as gobies and blennies (Hoese 1973; Springer and Gomon 1975; Carlton 1985), in fishes with extensive lateral-line systems (Janssen 1995; Jude 1997), and in the ubiquitous three-spined stickleback *Gasterosteus aculeatus* (Carlton 1985). In addition, we compare the success of two methods for sampling fishes in ballast tanks.

Materials and methods

We present new reports of fishes collected in an ongoing ballast survey, and previously reported but unidentified fishes from two studies (Carlton and Geller 1993; Smith et al. 1999). In general, fishes were collected from two kinds of ballast tanks aboard commercial vessels, cargo holds and dedicated ballast tanks. Cargo holds are large unpartitioned tanks with a mean ballast-water capacity of 15 000 to 19 000 MT (Smith et al. 1996); there are typically 1 to 2 floodable cargo holds per vessel. In contrast, dedicated ballast tanks are an order of magnitude smaller and are partitioned by vertical walls and horizontal platforms; a typical bulk cargo vessel may have 20 or more dedicated ballast tanks.

Table 1 Ballast-water sampling port, number of vessels (*n*), duration of study, and sampling methods for the three ballast-water sampling studies reported here (*Plankton net* samples collected in ballasted tanks; *Empty hold* samples collected from residual water and sediments in de-ballasted holds; *Y* yes; *N* no)

Sampling port	(n)	Years	Sampling method		Source
			Plankton net	Empty hold	
Coos Bay, Oregon	(159)	1986–1991	Y	N	Carlton and Geller (1993)
Baltimore, Maryland, and Norfolk, Virginia	(70)	1993–1994	Y	Y	Smith et al. (1999)
Baltimore, Maryland, and Norfolk, Virginia	(63)	1994–1996	Y	Y	Present study

In all three studies, two primary sampling techniques were used (Table 1). On all vessels ($n = 292$), we collected organisms with a plankton net hauled vertically through the tank at 0.5 $\mathrm{ms^{-1}}$ (3 replicate tows). On a subset of vessels ($n = 23$), we sampled for macrofauna by visually inspecting the residual water and sediments in the bottom of de-ballasted cargo holds. Vessel safety regulations generally prevented us from sampling dedicated ballast tanks in this way. On rare occasions, when fishes were seen at the water surface of full holds or tanks, we collected them by dip net ($n = 2$ vessels).

In the first of our studies, Carlton and Geller (1993) sampled cargo holds in 159 vessels arriving in Coos Bay, Oregon, USA, from Japan over a 5 yr period (Table 1). They sampled all tanks by plankton net only (80 µm mesh, 0.9 m long, 0.5 m diam). In the second study, Smith et al. (1999) surveyed vessels in the ports of Baltimore, Maryland, and Norfolk, Virginia, in Chesapeake Bay, USA. They sampled dedicated ballast tanks and cargo holds in 70 vessels arriving primarily from Europe and the Eastern Mediterranean. The present study reports 62 additional vessels sampled in Baltimore and Norfolk. In both Chesapeake Bay studies, we used plankton nets (80 µm mesh, 0.9 m long, 0.25 m diam), and we sampled some de-ballasted cargo holds. In all three studies, plankton samples were examined live under a dissecting microscope and preserved; macrofauna were preserved and photographed. Fishes were identified to the lowest taxonomic level possible. These identifications are referred to as taxa. In addition, we reviewed literature reports of fishes collected in ballast water.

For summary purposes, we grouped all collection data by fish family. For each family, both the number of species, and the number of reports, are discussed. The total number of reports in some families includes multiple collections of the same taxon from different vessels. Similarly, in summarizing literature on fish introductions attributed to ballast-water transport, we discuss both the number of species and the number of reports in each family. In some families, the total number of reports includes multiple introductions of the same species to different locations.

Results

Fishes collected in ballast water

Table 2 presents 28 new reports of fishes collected from cargo holds and ballast tanks. These reports comprise 17 taxa from 15 families, including the first ballast-water records for 13 fish taxa. Combining these data with reports from the literature yields a total of 54 reports of fishes in ballast water, based on all taxa aboard all vessels, including unidentified specimens. These reports include at least 31 identified taxa in 22 families (Table 2).

Of the new fish reports, all but two of the specimens survived ballast transport and were collected alive. Although most of the cargo holds and ballast tanks were filled in coastal waters at or near the port of departure, a few contained additional water (< 10% of tank capacity) added after departure (Table 2). Assuming, however, that the fishes were probably ballasted at or near the port of departure, they survived an average voyage length of 14.7 ± 5.1 d (mean ± 1 SD; range = 1 to 21 d; $n = 16$ vessels for which data were available). Of the 28 new fish collections, 8 were larval specimens. The remaining 20 reports were juveniles or adults: these were uniformly small (< 90 mm standard length), with the notable exception of the mullets (*Liza ramada*), which averaged 34.3 cm in total length ($n = 16$; range 29.4 to 39.2 cm).

Across all reports, most families (15 of 22) were collected only once, whereas seven were collected repeatedly (Fig. 1). Of these seven, three were represented by more than one species (Table 2): Gobiidae (nine reports of at least 6 species, including *Pomatoschistus lozanoi* sailing twice from Belgium to Baltimore); Clupeidae (five reports of at least 4 species, including two collections of the sprat *Sprattus sprattus*); and Osmeridae (2 species). The remaining four families reflected multiple collections of the same taxon, or of unidentified specimens (Table 2). The three-spined stickleback *Gasterosteus aculeatus* (Gasterosteidae), was collected five times in ballast water, from both the eastern and western North Atlantic. The jack, *Alepes djedaba* (Carangidae), arrived twice in Baltimore from the eastern Mediterranean, and a third, unidentified jack was collected along the same route. The anchovies *Engraulis* spp. (Engraulidae) sailed twice on the same North Atlantic shipping route. Two scorpionfishes (Scorpaenidae) were collected from ships arriving in Chesapeake Bay: *Centropogon australis* arrived from Australia, and an unidentified specimen from Israel (Table 2).

Nearly half the ballast-water fish reports (25 of 54) were for Northwest Atlantic ports, on ships sailing from Europe and the Mediterranean. The rest were for ships sailing to Europe (11), the Pacific Northwest (9), Australia (8), and along the Gulf of Mexico (1) (Table 2).

Fish introductions attributable to ballast water

At least 40 accidental introductions of 32 fish species in 11 families were attributable to ballast-water transport (Table 3). In addition to ballast transport, alternative

Table 2 Fishes collected from ballast water of commercial vessels *Ballast-water source* port or region where ballast tank was filled; *Destination port* in most cases port where ballast water was sampled, in some cases (*), ballast water was sampled some days before vessel arrived at destination port; + ballast tanks "topped up" with additional water loaded while vessel was underway (< 10% of total tank vol); *BW age* ballast-water age, i.e. number of days from ballasting to sampling; - no data; *AK* Alaska, USA; *CA* California, USA; *DE* Delaware, USA; *MD* Maryland, USA; *NSW* New South Wales, Australia; *OR* Oregon, USA; *R.* River; *TX* Texas, USA; *WA* Washington, USA

Taxon	Ballast water source	Destination port	BW age	Source
Petromyzontidae (lampreys)				
Petromyzon marinus	–	Germany	–	Gollasch and Dammer (1995), Gollasch et al. (1998), Gollasch (personal communication to MJW)
Anguillidae (fresh water eels)				
Anguilla anguilla	–	Germany	–	
Clupeidae (herrings, sprats)				
Clupea harengus	–	Germany	–	
Clupeonella sp. ^{a}	Belgium (Zeebrugge)$^{+}$	USA (Baltimore, MD)	17	Present study
Hyperlophus vittatus	Australia (Newcastle, NSW)	Australia (Port Hedland, NSW)*	1?	Middleton (1982)
Sprattus sprattus	NE Atlantic (Ireland)	USA (Baltimore, MD)	10	Smith et al. (1999), Present study
S. sprattus	–	Germany	–	Gollasch and Dammer (1995), Gollasch et al. (1998), Gollasch (personal communication to MJW)
Unidentified larval clupeid or atherinid	USA (Mississippi R.)	USA (Baltimore, MD)	12	Present study
Engraulidae (anchovies)				
Engraulis encrasicolus	Israel (Ashdod)$^{+}$	USA (Baltimore, MD)	17	Smith et al. (1999), Present study
?*Engraulis* sp. (larva)	Israel (Ashdod)$^{+}$	USA (Baltimore, MD)	21	Present study
Osmeridae (smelts)				
Allosmerus elongatus	–	Germany	–	Gollasch and Dammer (1995) Gollasch et al. (1998), Gollasch (personal communication to MJW)
Osmerus eperlanus	–	Germany	–	
Atherinidae (silversides)				
Atherina (= Hepsetia) boyeri	Belgium (Zeebrugge)$^{+}$	USA (Baltimore, MD)	17	Present study
Gasterosteidae (sticklebacks)				
Gasterosteus aculeatus	Germany (Weser R.)	USA (Wilmington, DE)	12	Carlton et al. (1982)
G. aculeatus	Canada (St. Lawrence R.)	USA (Baltimore, MD)	7	Smith et al. (1999), Present study
G. aculeatus	Belgium (Zeebrugge)$^{+}$	USA (Baltimore, MD)	17	Present study
G. aculeatus	Netherlands (IJmuden)	USA (Baltimore, MD)	21	
G. aculeatus	–	Germany	–	Gollasch and Dammer (1995), Gollasch et al. (1998), Gollasch (personal communication to MJW)
Syngnathidae (pipefishes)				
Syngnathus rostellatus	–	Germany	–	
Scorpaenidae (scorpionfishes)				
Centropogon australis	Australia (Newcastle, NSW)	Australia (Port Hedland, NSW)*	1?	Middleton (1982)
Unidentified juvenile scorpaenid (dead)	Israel (Hadera)	USA (Baltimore, MD)	–	Present study
Hexagrammidae (greenlings)				
Unidentified larval hexagrammid	Japan (Kushiro)	USA (Coos Bay, OR)	13	Carlton and Geller (1993), Present study
Cottidae (sculpins)				
Unidentified larval cottid	Japan (Kushiro)	USA (Coos Bay, OR)	13	
Teraponidae (grunter perches)				
Terapon (= Therapon) jarbua	Japan (Yokohama)	Australia (Eden, NSW)	14	Williams et al. (1988)

Carangidae (jacks)				
Alepes djedaba	Israel (Ashdod)$^{+}$	USA (Baltimore, MD)	15	Smith et al. (1999), Present study
A. djedaba	Israel (Hadera)	USA (Baltimore, MD)	–	Present study
Unidentified carangid	Israel (Hadera)	USA (Baltimore, MD)	–	
Siganidae (rabbitfishes)				
Siganus rivulatus	Israel (Ashdod)	USA (Baltimore, MD)	21	
Mugilidae (mullets)				
Liza ramada	Israel (Ashdod)	USA (Baltimore, MD)	21	
Blennidae (combtooth blennies)				
Petroscirtes breviceps	Japan	Australia	–	Williams (1977), Carlton (1985)
Ammodytidae (sand lances)				
Ammodytes personatus (larva)	Japan (Bunga Suido Straits)	USA (Coos Bay, OR)	16	Carlton and Geller (1993), Present study
Gobiidae (gobies)				
Favonigobius sp.	Australia (Newcastle)	Australia (Port Hedland, NSW)*	1?	Middleton (1982)
Gobius niger (= *G. jozo*)	Israel (Ashdod)	USA (Baltimore, MD)	17	Present study
Pomatoschistus lozanoi	Belgium (Zeebrugge)	USA (Baltimore, MD)	13	Smith et al. (1999), Present study
P. lozanoi	Belgium (Zeebrugge)$^{+}$	USA (Baltimore, MD)	17	Present study
P. minutus	–	Germany	–	Gollasch and Dammer (1995), Gollasch et al. (1998), Gollasch (personal communication to MJW)
Pomatoschistus sp.	Belgium (Antwerp)	USA (Baltimore, MD)	14	Present study
Ptereleotris sp.	Japan (Yokohama)	Australia (Eden, NSW)	15	Williams et al. (1998)
Tridentiger trigonocephalus	Australia	–	–	Paxton and Hoese (1985)
Unidentified gobiid	Belgium (Antwerp)	USA (Baltimore, MD)	14	Present study
Bothidae (left-eye flounders)				
Pseudorhombus arsius	Australia (Newcastle, NSW)	Australia (Port Hedland, NSW)*	1?	Middleton (1982)
Pleuronectidae (right-eye flounders)				
Unidentified larval ?pleuronectid (dead)	Japan (Iwakuni, Inland Sea)	USA (Coos Bay, OR)	16	Carlton and Geller (1993), Present study
Soleidae (soles)				
Unidentified juvenile soleid	Belgium (Zeebrugge)	USA (Baltimore, MD)	13	Smith et al. (1999), Present study
Monacanthidae (filefishes)				
Stephanolepis diaspros	Israel (Hadera)	USA (Baltimore, MD)	–	Present study
Unidentified larvae from 2 tanks on 1 vessel	Israel (Hadera)	USA (Baltimore, MD)*	1,2	Present study
Unidentified fishes from 3 vessels	Japan	USA (Tacoma and Pt. Angeles, WA)	11–15	Kelly (1993)
Unidentified fish eggs and larvae from 1 vessel	USA (Florida/Gulf of Mexico)	USA (Corpus Christi, TX)	4	Carlton et al. (1982)
Unidentified fishes from 1 vessel	Scotland	Iceland	2	
Unidentified fishes from 1 vessel[b]	Singapore (Persian Gulf)	England (Grimsby)	–	Wheeler (1958)
Unidentified fish eggs and larva from 1 vessel	Italy (Trieste)	USA (Baltimore, MD)	15	Smith et al. (1999), Present study
Unidentified fishes from 2 vessels	USA (San Francisco Bay, CA)	USA (Port Valdez, AK)	6	Ruiz and Hines (1997)

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[a] Tentatively identified as *C. cultiventris* or *C. engrauliformes* (V. Springer personal communication)

[b] Fish were captured alive at docks (i.e. not directly from ballast water) after release from hold of a dredge carrier

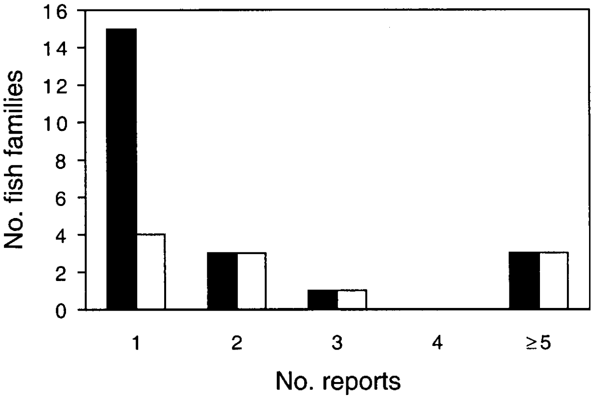

Fig. 1 Frequency of ballast-mediated transport (*black bars*; $n = 48$ records), and introduction (*open bars*; $n = 43$ records) of fish families. Bars represent number of fish reports, including multiple reports of same species collected from different vessels or introduced to different locations

dispersal mechanisms such as ship-hull fouling, canals, and intentional release were suggested in some cases. For example, the invasion of the Laurentian Great Lakes by *Petromyzon marinus* (sea lamprey) has been attributed to several possible pathways, including ballast-water transport (Lamsa et al. 1980), and ship-fouling transport, bait-stocking or simply swimming through canals (e.g. Lamsa et al. 1980; Morman et al. 1980; Mills et al. 1993). Similarly, anguillid eel introductions to California were initially attributed to ballast transport (Skinner 1971), and later, following subsequent reports, to seafood imports and fish-farm escapes (McCosker 1989; Williamson and Tabeta 1991). Fish introductions attributed in the literature to possible ship-hull transport, but not to ballast transport, are not dealt with here.

Among the 11 families introduced via ballast water, 4 were introduced only once, and 7 were introduced on multiple occasions (Fig. 1). The three most commonly introduced families were the Gobiidae, Blenniidae and Pleuronectidae (Table 3). Goby introductions occurred over a global scale, with introductions to the Pacific, the Atlantic, the Arabian Gulf, and the Laurentian Great Lakes. Two Asian species, *Acanthogobius flavimanus* and *Tridentiger trigonocephalus*, each established nonindigenous populations in San Francisco Bay and Los Angeles Harbor, California, and in Sydney Harbour, Australia. Two additional gobies, *T. bifasciatus* and *T. barbatus* have arrived more recently in San Francisco Bay (Table 3). Blennies were introduced on eight occasions (6 species), including three introductions of the Indo-Pacific *Omobranchus punctatus* to Mozambique, the Caribbean, and the Panama Canal (Table 3). The seven pleuronectid introductions consist of six separate reports of the European flatfish *Platichthys flesus* in the Laurentian Great Lakes, and one introduction of the plaice *Pleuronectes platessa* to the Red Sea (Table 3). Of the 40 introductions attributed to ballast transport, 24 (60%) were reported to have established persistent populations (Table 3). Together, gobies and blennies accounted for more than half of these established introductions (11 and 6, respectively).

Inoculation vs invasion

Only two species, the stickleback *Gasterosteus aculeatus* and the goby *Tridentiger trigonocephalus*, have been both collected in ballast water (Table 2) and introduced via ballast transport (Table 3). At the family level, however, there is more striking correspondence between the frequency of inoculation (Phase 1) and the frequency of introduction (Phase 2). We restricted our comparison to those five families that were transported or introduced on more than four occasions: Gobiidae, Clupeidae, Gasterosteidae, Blenniidae, and Pleuronectidae (Fig. 1, Tables 2 and 3). Gobies were the family most frequently collected from ballast water, and the most frequently introduced and established (Fig. 2). Blennies were also introduced and established on multiple occasions, but were collected only once from ballast water (Fig. 2). Sticklebacks (Gasterosteidae) were collected frequently from ballast water (five collections of *Gasterosteus aculeatus*), but introduced and established only twice (Fig. 2). Clupeids, too, were commonly collected, but there are no reported ballast-mediated introductions for this family (Fig. 2). In contrast, pleuronectids were frequently introduced (although never established), but were collected only once from ballast water.

Collection methods

We collected fishes from 18 of the 292 vessels. In some de-ballasted holds, fishes of several species together numbered hundreds. On most vessels (13 of 18) we collected only one taxon, on three vessels we collected 2 taxa, and on two vessels 4 taxa. Of the 292 ships, 23 were sampled both by plankton net and by visual inspection of de-ballasted holds (Table 4). The frequency of fish collection in empty holds (8 of 23) was significantly greater than that in plankton net samples in the same holds (1 of 23) (Fisher's exact test $p = 0.022$, table-wide $\alpha = 0.05$; sequential Bonferroni corrected $\alpha = 0.016$). The remaining 269 vessels were sampled by plankton net alone. Here too, the frequency of fish collection (8 of 269) was significantly lower than from the holds sampled by visual inspection (8 of 23) (Fisher's exact test $p = 0.000$, table-wide $\alpha = 0.05$; sequential Bonferroni corrected $\alpha = 0.016$) (Table 4). Of the fishes collected from empty tanks significantly more were postlarval (12 of 15 in 23 holds) than from plankton tows (2 of 9 from 269 ships) (Fisher's exact test $p = 0.008$). In addition to these two sampling methods, serendipitous collections of single species were made from the water surface of an open tank on three vessels (*Alepes djedaba*, *Sprattus sprattus*, and *Gasterosteus aculeatus*; this last species was collected also by plankton net from the same tank).

Table 3 Fish introductions attributed to ballast-water transport (including attributions to transport in bilge water or other seawater systems) [*Y*, *N*, *established* presence of persistent population (*Y* yes; *N* no; ? unknown)] (*CA* California; *SFB* San Francisco Bay; *WA* Western Australia; *NSW* New South Wales) Review papers cited where possible

Taxon	Introduced		Established	Source
	from	to		
Petromyzontidae (sea lampreys)				
Petromyzon marinus	Atlantic drainage?	Laurentian Great Lakes	Y	Lamsa et al. (1980)
Anguillidae (freshwater eels)[a]				
Anguilla anguilla	Western Europe	USA (SFB, CA)	N	Carlton (1985)
A. rostrata	Northwest Atlantic	USA (SFB, CA)	N	
Cyprinodontidae (killifishes)				
Cyprinodon variegatus	Northwest Atlantic	USA (WA)	N	
Lucania parva	Northwest Atlantic	USA (OR)	Y	
L. parva	Northwest Atlantic	USA (SFB, CA)	Y	
Gasterosteidae (sticklebacks)				
Apeltes quadracus	Eastern Canada	Laurentian Great Lakes	Y	Holm and Hamilton (1988)
Gasterosteus aculeatus	North Atlantic	Laurentian Great Lakes	Y	Carlton (1985)
Percidae (perch)				
Gymnocephalus cernuus	Europe	Laurentian Great Lakes	Y	Carlton and Geller (1993)
Sparidae (porgies)				
Sparidentex hasta	Arabian Sea	Australia (Perth, WA)	?	Jomes (1992), Carlton and Geller (1993)
Blenniidae (combtooth blennies)				
Hypleurochilus aequippinis	East and West Atlantic	Panama Canal	Y	Carlton (1985)
Hypsoblennius ionthas	Southern USA	USA (Hudson R.)	?	
Lupinoblennius dispar	West Central Atlantic	Panama Canal (Pacific side)	Y	
Omobranchus ferox	Indo-West Pacific	Mozambique	Y	
O. punctatus	Indo-West Pacific	Mozambique	Y	
O. punctatus	Indo-West Pacific (India)	Venezuela and Trinidad	Y	
O. punctatus	Venezuela or Trinidad	Atlantic Panama and Canal	Y	
Parablennius thysanius	Philippines, Indian Ocean	USA (Hawaii)	?	Carlton (1985), Carlton and Geller (1993)
Gobiidae (gobies)				
Acanthogobius flavimanus	Asia	USA (SFB, CA)	Y	Carlton (1985)
A. flavimanus	Asia	Australia (Sydney, NSW)	Y	
A. flavimanus	Asia or USA (SFB)	USA (Los Angeles, CA)	Y	
Barbulifer ceuthoecus	West Central Atlantic	Pacific Panama	?	
Gobiomorphus coxii	Australia (NSW)	Australia (Sydney, NSW)	?	Jones (1992)
Gobionellus hastatus	Southern USA	USA (Hudson R.)	?	Carlton (1985)
Gobiosoma nudum	West Central Pacific	Atlantic Panama	?	
Lophogobius cyprinoides	West Central Atlantic	Panama Canal (Pacific side)	Y	
Neogobius melanostomus	Black/Caspian Seas	Laurentian Great Lakes	Y	Carlton and Geller (1993)
Proterorhinus marmoratus	Black/Caspian Seas	Laurentian Great Lakes	Y	
Rhinogobius brunneus	Asia	Arabian Gulf	?	
Tridentiger trigonocephalus	Asia	USA (SFB, CA)	Y	Carlton (1985)
T. trigonocephalus	Asia	Australia (Sydney, NSW)	Y	Carlton (1985), Paxton and Hoese (1985), Jones (1992)
T. trigonocephalus	Asia	USA (Los Angeles, CA)	Y	Carlton (1985)
T. bifasciatus	Asia	USA (SFB, CA)	Y	Matern and Fleming (1995) Matern (personal communication to MJW)
T. barbatus	Asia	USA (SFB, CA)	Y	Fleming (1998), Fleming (personal communication to MJW)
Mugiligobius parvus	Taiwan, Philippines	Hawaii	?	Carlton and Geller (1993)
Eleotridae (sleeper gobies)				
Butis koilomatodon	Indo-West Pacific	Panama Canal	?	Carlton (1985), Carlton and Geller (1993)
B. koilomatodon	Indo-West Pacific	Nigeria, Cameroon	Y	Carlton and Geller (1993)
Pleuronectidae (right-eye flounders)				
Platichthys flesus[b]	Western Europe	Laurentian Great Lakes	N	Carlton (1985)
Pleuronectes platessa	Western Europe	Red Sea (Gulf of Elat)	?	Hensley (1983)
Percoidei (genus incertae sedis)[c]				
Lateolabrax japonicus	Japan	Australia	N	Paxton and Hoese (1985)

[a] McCosker (1989) considers other pathways more likely than ballast transport for Atlantic eels introduced to the northeast Pacific

[b] *Platichthys flesus* was introduced to the Great Lakes on six independent occasions (Carlton et al. 1995)

[c] Considered a separate family for summary purposes

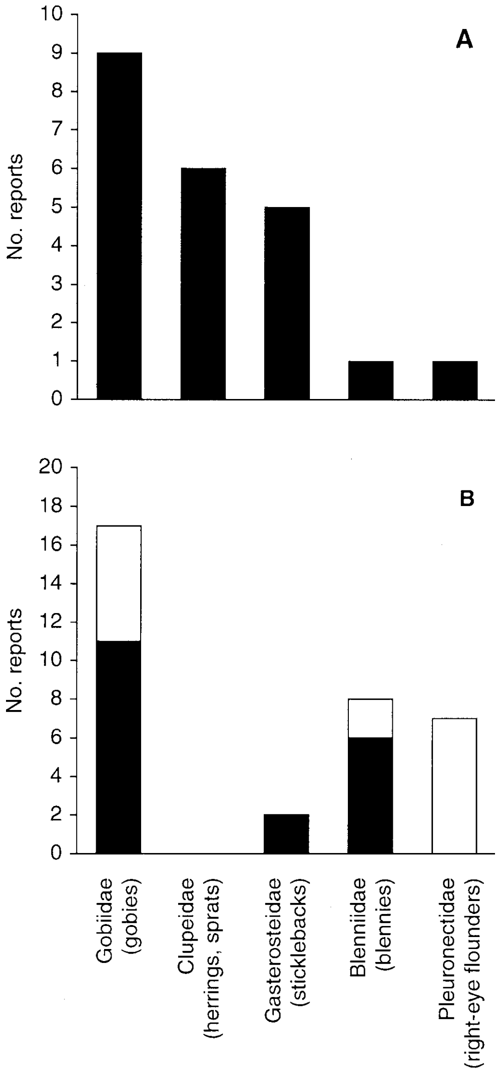

Fig. 2 The five fish families most commonly transported (**A**) and introduced (**B**) via ballast water. Reported introductions (**B**) are divided into those established (*black bars*) and those whose establishment is uncertain or has not occurred (*open bars*)

Discussion

Forty introductions of 32 fish species have been attributed to ballast-water transport world-wide, yet we found little overlap between these reported species and the species collected from ballast tanks and cargo holds. The disparity between the two data sets probably reflects both systematic under-reporting and undersampling. Under-reporting results from the relatively recent recognition that decades of ballast transport have provided a major pathway for marine and aquatic introductions (Carlton 1985). Undersampling of ballast water occurs both during the sampling of tanks and during the sampling on global shipping routes. Most ballast-water studies, including our own, relied primarily on plankton-tow samples. These samples typically filter only a small fraction of the water in a tank (e.g. < 1% of most tanks, Smith et al. 1999); worse yet, fishes may actively avoid the net openings (Carlton and Geller 1993). In contrast, the organisms left in the bottom of a de-ballasted cargo hold represent the crudely filtered contents of most of the tank volume. We found that visual inspection of this residue yielded a significantly greater frequency and diversity of fishes, especially of identifiable postlarval specimens. On a global scale, > 7000 species may be transported per day by ballast water; thus, the probability of finding the same range of fish species in the relatively few ships sampled is low (Carlton 1999). In short, vastly more fishes must be transported – in terms of both abundance and diversity – than have been sampled. These reporting and sampling limitations make it difficult to evaluate relationships between transfer and invasion at the species level. At the family level, however, certain patterns emerge.

Table 4 Comparison of ballast-water sampling methods in three studies reported (Table 1). Of 292 vessels sampled, 269 were sampled by plankton net only. On 23 additional vessels, ballast tank was sampled with plankton net when full, and by visual inspection of de-ballasted hold when empty. Two reports of fish collected by dip net have been omitted. [*Significant differences among methods (see "Results – Collection methods"]

	Two methods		One method:
	Plankton net	Empty hold	Plankton net only
No. ships sampled	23	23	269
No. ships that collected fish	1	8	8
Percent ships with fish*	4.3	34.8	3.0
Total fish records	2	15	9
Percent postlarval fish records*	100	80	22

Why are certain families successful invaders?

Taxon-specific traits not typically associated with invasive ability may increase dispersal frequency and, therefore, invasion success. In addition, high abundance and a broad range (which may include previous successful invasions) may contribute to the statistical likelihood of dispersal and invasion. Multiple transports or introductions were documented for five families: Gobiidae, Clupeidae, Gasterosteidae, Blenniidae, and Pleuronectidae. To test for traits contributing to invasion success, we should ideally compare characteristics and abundances of taxa that survive each phase to the entire pool of taxa present at that phase (Carlton 1996; Vermeij 1996). Unfortunately, such data are rarely available. Nonetheless, certain traits do correlate with dispersal success.

Taxon-specific traits

Gobies and blennies were the most often-reported ballast-water dispersers and invaders. The crevicolous nature of gobies when seeking refuge and laying eggs may predispose them to ballast-water transport, particularly if the ballast-intake grates on ship hulls present appealing crevices (Hoese 1973; Springer and Gomon 1975; Carlton 1985). Rainer's (1995) observation of gobies darting in and out of hull gratings in an Australian port further supports this hypothesis. Although the same behavior has been implicated in blenny introductions (Hoese 1973; Springer and Gomon 1975; Carlton 1985), this family has been collected only once from ballast water. Their infrequent occurrence may reflect a geographic sampling bias: none of the sampled ships arrived from ports in the Indo-West Pacific, the global region of highest blenny diversity and abundance (Zander 1984).

Once on board a vessel, a fish must survive transport in a dark ballast tank. Gobies are well represented among cave fishes, in part because of their specialized lateral-line system (e.g. Parzefall 1986), which may be a pre-adaptation to surviving ballast transport (Janssen 1995; Jude 1997). The same has been suggested for the nocturnal ruffe *Gymnocephalus cernuus*, another invader of the Laurentian Great Lakes (Janssen 1995, 1997). However, the repeated ballast-transport survival of the stickleback *Gasterosteus aculeatus* indicates that even visual predators can survive transoceanic voyages.

Upon release, the crevicolous nature of gobies and blennies may again predispose them to survive well in habitats in and around ports (e.g. dock pilings, bottom debris). In these two families, traits not typically associated with successful invaders may nonetheless contribute to invasion success by increasing the frequency of dispersal. For gobies, the relatively high frequency of transport alone may explain the frequency of their invasions. The same may hold for blennies, but further sampling over a broader geographic range is needed to establish their transport frequency.

Abundance and ubiquity

Carlton (1985) predicted that *Gasterosteus aculeatus* would prove to be a regular member of the ballast-water biota. Our data show that this fish is the most commonly found species in ballast surveys to date, and has been collected from vessels arriving on both sides of the north Atlantic. A common species, globally distributed in freshwater, estuarine, coastal, and open-marine temperate habitats (Bell and Foster 1994), its ubiquity presumably increases its likelihood of ballast transport. Despite a high potential for extensive and repeated transport, only two records exist of successful stickleback introductions. Interestingly, however, this species possesses many of the characters typically associated with invaders, such as broad physiological tolerance and diet, flexible reproductive strategies, and rapid evolution (Bell and Foster 1994). A high frequency of ballast transport in this century may have contributed both to under-reporting of past introductions and to some of the difficulties of phylogenetic placement described for populations of this species (Haglund et al. 1992; Bell and Foster 1994).

Why have certain families not invaded?

Pleuronectids have been collected only once in ballast water, although they have been introduced on multiple occasions. These benthic fish may have been missed both by plankton net samples and during visual inspection of de-ballasted tanks because of their close association with the tank bottom and their cryptic coloration. Despite their multiple introductions, this group is not known to have established any nonindigenous populations. Six of the seven pleuronectid reports were independent introductions of *Platichthys flesus* to the Great Lakes, where this estuarine species may be unable to reproduce. The chances of a successful invasion might be improved with a better habitat match between donor and recipient regions.

The high-density schooling behavior of clupeids may contribute to their entrainment and survival in ballast tanks. In addition, their multiple collections may reflect in part their prevalence in the northeast Atlantic, where much of the sampled ballast water originated. It is unclear why there are no reported introductions for this family; possibly, the abiotic conditions of port waters (e.g. low salinities in Baltimore, Maryland) or insufficient population sizes (e.g. see Allee 1931) have inhibited invasions.

Ballast water is an important and underestimated vector for the transfer and introduction of fishes. Only by sampling de-ballasted tanks can we obtain a more complete picture of fish (and other macrofaunal) transport. Fish families differ in their frequency of ballast-mediated transport, introduction, and establishment. The occurrence of fishes in ballast water does not correlate with invasion success at the species level, but does do so to some degree at the family level. The frequency of ballast transport in some families may be increased by unexpected, taxon-specific traits not typically associated with invasion success. In other cases, high abundance and a broad global range may contribute to higher transport frequency. Simply by increasing the frequency of dispersal (Phase 1), these traits may increase the chances of subsequent introduction and establishment (Phases 2 and 3). Determining both the relative abundance of species and the characteristics contributing to their success at each invasion phase will allow the development of a better predictive framework of invasions in general, and of ballast water invasions in particular.

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References

Allee WC (1931) Animal aggregations. A study in general sociology. University of Chicago, Chicago, Illinois

Baker HG, Stebbins GL (eds) (1965) The genetics of colonizing species. Academic Press, London

Baldwin RP (1992) Cargo vessel ballast water as a vector for the spread of toxic phytoplankton species to New Zealand. J R Soc NZ 22: 229–242

Baltz DM (1991) Introduced fishes in marine systems and inland seas. Biol Conserv 56: 151–177

Bell MA, Foster SA (eds) (1994) The evolutionary biology of the threespine stickleback. Oxford University Press, Oxford

Carlton JT (1985) Transoceanic and interoceanic dispersal of coastal marine organisms: the biology of ballast water. Oceanogr mar Biol A Rev 23: 313–371

Carlton JT (1996) Pattern, process, and prediction in marine invasion ecology. Biol Conserv 78: 97–106

Carlton JT (ed) (1998) Ballast water: ecological and fisheries implications. Co-op Res Rep int Counc Explor Sea 224: 1–146

Carlton JT (1999) The scale and ecological consequences of biological invasions in the world's oceans. In: Sandlund OT, Schei PJ, Viken A (eds) Invasive species and biodiversity management. Kluwer Academic Publishers, New York, pp 195–212

Carlton JT, Geller JB (1993) Ecological roulette: the global transport of nonindigenous marine organisms. Science, NY 261(5117): 78–82

Carlton JT, Navarret AM, Mann R (1982) Biology of ballast water: the role of ballast water in the transoceanic dispersal of marine organisms. National Science Foundation, Division of Applied Research Department of Biology, Woods Hole Oceanographic Institution, Woods Hole (Final Project Report; Grant No. DAR-8008450)

Carlton JT, Reid DM, van Leeuwen H (1995) Shipping study. The role of shipping in the introduction of non-indigenous aquatic organisms to the coastal waters of the United States (other than the Great Lakes) and an analysis of control options. (The National Sea Grant College Program/Connecticut Sea Grant Project R/ES-6. Department of Transportation) United States Coast Guard, Washington, DC [Rep No. CG-D-11–95. Government Accession Number AD-A294809. xxviii + 213 pages and Appendices A-I (122 pages)]

Chapin III FS, Sala OE, Burke IC, Grime JP, Hooper DU, Lauenroth WK, Lombard A, Mooney HA, Mosier AR, Naeem S, Pacala SW, Roy J, Steffen WL, Tilman D (1998) Ecosystem consequences of changing biodiversity. BioSci 48: 45–52

Cohen AN, Carlton JT (1995) Biological study. Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco Bay and Delta. US Department of Commerce National Technical Information Service, Washington, DC (Report for US Fish and Wildlife Service, Washington, DC, and National Sea Grant College Program, Connecticut Sea Grant; NTIS Rep No. PB96-166525, 246 pp. + Appendices)

Ehrlich PR (1986) Which animal will invade? In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, pp 79–95

Ehrlich PR (1989) Attributes of invaders and the invading process: vertebrates. In: Drake JA, Mooney HA, Di Castri F, Groves RH, Kruger FJ, Rejmánek F, Williamson M (eds) Biological invasions: a global perspective. Scientific Committee on Problems of the Environment, SCOPE Rep. No. 37. John Wiley & Sons, New York, pp 315–328

Elton CS (1958) The ecology of invasions by animals and plants. Methuen & Co, Ltd, London

Fleming K (1998) Exotic goby takes up residence in estuary. Interagency Ecological Program for the Sacramento-San Joaquin Estuary. Department of Water Resources, Environmental Services Office, Sacremento, California (IEP Newsl 11)

Fuller PM, Nico LG, Williams JD (1999) Nonindigenous fishes introduced into inland waters of the United States. Spec Publs Am Fish Soc 27: 1–613

Golani D (1993) The sandy shore of the Red Sea – launching pad for Lessepsian (Suez Canal) migrant fish colonizers of the eastern Mediterranean. J Biogeogr 20: 579–585

Golani D (1996) The marine ichthyofauna of the eastern Levant – history, inventory, and characterization. Israel J Zool 42: 15–55

Gollasch S, Dammer M (1995) First results of the German research project: invasion of non-indigenous marine species into the North and Baltic Sea via ship's ballast water: investigations on the ecological threat. (Meeting of the ICES Working Group on Introductions and Transfers of Non-indigenous Organisms) International Council for the Exploration of the Sea, Kiel, Germany

Gollasch S, Dammer M, Lenz J, Andres HG (1998) Nonindigenous organisms introduced via ships into German waters. Co-op Res Rep int Counc Explor Sea 224: 50–64

Haglund TR, Buth DG, Lawson R (1992) Allozyme variation and phylogenetic relationships of Asian, North American, and European populations of the threespine stickleback, *Gasterosteus aculeatus*. Copeia 1992(2): 432–443

Hallegraeff GM, Bolch CJ (1991) Transport of toxic dinoflagellate cysts via ships' ballast water. Mar Pollut Bull 22: 27–30

Hensley DA (1993) Two new flatfish records from the Red Sea, an Indo-Pacific samarid (*Samariscus inornatus*) and the European plaice (*Pleuronectes platessa*). Israel J Zool 39: 371–379

Hoese DF (1973) The introduction of the gobiid fishes *Acanthogobius flavimanus* and *Tridentiger trigonocephalus* into Australia. Koolewong 2(3): 3–5

Holm E, Hamilton JG (1988) Range extension for the fourspine stickleback, *Apeltes quadracus*, to Thunder Bay, Lake Superior. Can Fld Nat 102: 653–656

Janssen J (1995) Dark ballast water, lateral lines, and fish invasions. Fifth International Zebra Mussel and other Aquatic Nuisance Organisms Conference held February 21–24 in Toronto, Canada (Unpublished Abstract)

Janssen J (1997) Comparison of response distance to prey via the lateral line in the ruffe and yellow perch. J Fish Biol 51: 921–930

Jones DS (1992) A review of Australian fouling barnacles. Asian mar Biol 9: 89–100

Jude DJ (1997) Round gobies: Cyberfish of the third millennium. Great Lakes Res Rev 3: 27–34

Kelly JM (1993) Ballast water and sediments as mechanisms for unwanted species introductions into Washington state. J Shellfish Res 12: 405–410

Lamsa AK, Rovainen CM, Kolenosky DP, Hanson LH (1980) Sea lamprey (*Petromyzon marinus*) control – where to from here? Report of the SLIS Control Theory Task Force. Can J Fish aquat Sciences 37: 2175–2192

Lever C (1996) Naturalized fishes of the world. Academic Press, San Diego

Lodge DM (1993) Biological invasions: lessons for ecology. Trends Ecol Evolut 8: 133–136

Matern SA, Fleming KJ (1995) Invasion of a third Asian goby, *Tridentiger bifasciatus*, into California. Calif Fish Game 81: 71–76

McCosker JE (1989) Freshwater eels (family Anguillidae) in California: current conditions and future scenarios. Calif Fish Game 75: 4–10

Medcof JC (1975) Living marine animals in a ship's ballast water. Proc natn Shellfish Ass 65: 11–12

Middleton MJ (1982) The Oriental goby, *Acanthogobius flavimanus* (Temminck and Schlegel), an introduced fish in the coastal waters of New South Wales, Australia. J Fish Biol 21: 513–523

Miller PJ, Wright J, Wongrat P (1989) An Indo-Pacific goby (Teleostei: Gobioidei) from West Africa, with systematic notes on *Butis* and related eleotridine genera. J nat Hist 23(2): 311–324

Mills EL, Leach JH, Carlton JT, Secor CL (1993) Exotic species in the Great Lakes: a history of biotic crises and anthropogenic introductions. J Great Lakes Res 19: 1–54

Morman RH, Cuddy DW, Rugen PC (1980) Factors influencing the distribution of sea lamprey (*Petromyzon marinus*) in the Great Lakes. Can J Fish Aquat Sciences 37: 1811–1826

Moyle PB (1986) Fish introductions into North America: patterns and ecological impact. In: Mooney HA, Drake JA (eds) Ecology of biological invasions of North America and Hawaii. Springer-Verlag, New York, pp 27–43

Moyle PB, Light T (1996) Biological invasions of fresh water: empirical rules and assembly theory. Biol Conserv 78: 149–161

Moyle PB, Vondracek B (1985) Persistence and structure of the fish assemblage in a small California stream. Ecology 66: 1–13

National Research Council (1996) Stemming the tide: controlling introductions of nonindigenous species by ships' ballast water. National Academy of Sciences, Washington, DC

Office of Technology Assessment (1993) Harmful nonindigenous species in the United States. US Congress, Office of Technology, Washington, DC

Parzefall J (1986) Behavioural ecology of cave-dwelling fishes. In: Pitcher TJ (ed) The behavior of teleost fishes. Johns Hopkins University Press, Baltimore, pp 433–458

Paxton JR, Hoese DF (1985) The Japanese sea bass, *Lateolabrax japonicus* (Pisces, Percichthyidae), an apparent marine introduction into eastern Australia. Jap J Ichthyol 31: 369–372

Pollard DA, Hutchings PA (1990) A review of exotic marine organisms introduced to the Australian region. I. Fishes. Asian Fish Sci 3: 205–221

Rainer SF (1995) Potential for the introduction and translocation of exotic species by hull fouling: a preliminary assessment. Centre for the Research on Introduced Marine Pests (CRIMP) Tech Rep Div Fish Oceanogr CSIRO Aust 1: 1–18

Randall JE (1987) Introductions of marine fishes to the Hawaiian Islands. Bull mar Sci 41: 490–502

Reichard SH, Hamliton CW (1997) Predicting invasions of woody plants introduced into North America. Conserv Biol 11: 193–203

Rejmánek M, Richardson DM (1996) What attributes make some plant species more invasive? Ecology 77: 1655–1661

Ruesink JL, Parker IM, Groom MJ, Kareiva PM (1995) Reducing the risks of nonindigenous species introductions: guilty until proven innocent. BioSci 45: 465–477

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 P, Hines AH, Grosholz ED (1999) Non-indigenous species as stressors in estuarine and marine communities: assessing invasion impacts and interactions. Limnol Oceanogr 44: 950–972

Ruiz GM, Hines AH (1997) The risk of nonindigenous species invasion in Prince William Sound associated with oil tanker traffic and ballast water management: pilot study. Regional Citizens' Advisory Council of Prince William Sound, Valdez, Alaska (Rep. No. 632f.97.1)

Schoener TW, Spiller D (1995) Effect of predators and area on invasion: an experiment with island spiders. Science, NY 267: 1811–1813

Skinner JE (1971) *Anguilla* recorded from California. Calif Fish Game 57: 76–79

Smith LD, Wonham MJ, McCann LD, Reid DM, Ruiz GM, Carlton JT (1996) Shipping study. II. Biological invasions by nonindigenous species in United States waters: quantifying the role of ballast water and sediments. Parts I and II. United States Coast Guard, Washington, DC (Rep. No. CG-D-02-97)

Smith LD, Wonham MJ, McCann LD, Ruiz GM, Hines AH, Carlton JT (1999) Invasion pressure to a ballast-flooded estuary and an assessment of inoculant survival. Biol Invasions 1: 67–87

Springer VG, Gomon MF (1975) Revision of the blenniid fish genus *Omobranchus* with descriptions of three new species and notes on other species of the tribe Omobranchini. Smithson Contr Zool 177: 1–135

Vermeij G (1991) When biotas meet: understanding biotic interchange. Science, NY 253(5024): 1099–1104

Vermeij G (1996) An agenda for invasion biology. Biol Conserv 78: 3–9

Wheeler AC (1958) The identity of the British fish *Parviclinus spinosus*. Proc zool Soc Lond 130: 253–256

Williams RJ (1977) Nine months of ballast water studies. Aust mar Sci Bull 60: p. 9

Williams RJ, Griffiths FB, Van der Wal EJ, Kelly J (1988) Cargo vessel ballast water as a vector for the transport of non-indigenous marine species. Estuar, cstl Shelf Sci 26: 409–420

Williamson M (1996) Biological invasions. Chapman & Hall, New York

Williamson GR, Tabeta O (1991) Search for *Anguilla* eels on the west coast of North America and on the Aleutian and Hawaiian Islands. Jap J Ichthyol 38: 315–317

Zander CD (1984) Blenniidae. In: Whitehead PJP, Bauchot ML, Hureau J-C, Nielsen J, Tortonese E (eds) Fishes of the northeastern Atlantic and the Mediterranean. Vol. 3. UNESCO, Rome, p. 1096