Chapter 33
Invasions of Estuaries vs the Adjacent Open Coast: A Global Perspective

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33.1 Habitat Differences in Marine Invasion Rates

Invasions by alien species have been reported from every marine habitat where surveys have been conducted for them. Conspicuous examples from around the globe include the brown alga *Sargassum mangarevense* in tropical coral reef systems (Andréfouët et al. 2004), the bivalve *Mytilus galloprovincialis* along temperate rocky shores (Steffani and Branch 2003), and the reef-building polychaete, *Ficopomatus enigmaticus* in estuaries (Schwindt et al. 2004). Despite numerous examples of marine invaders from a variety of habitats, little is known about how invasion rates of entire assemblages of organisms compare between different marine habitat types. And indeed most marine habitats have not been thoroughly surveyed – the majority of our understanding of marine invasions comes from shallow near-shore environments.

Some studies have attempted to quantify habitat differences in marine invasions, examining assemblages (both natives and aliens) at different scales. Within estuarine ecosystems, focus has been on comparisons between different salinities and substrates. (In this chapter an estuary is considered to be a ‘partly enclosed body of water by the coast in which sea water and fresh water mix‘ (Little 2000).) Wolff (1973) examined the benthic macroinvertebrates of four major estuaries in the Netherlands. He found that in the high salinity parts of these estuaries about 2% of the species were alien, in the brackish part about 20%, and in the tidal freshwater part about 8%. In non-tidal brackish waters the share of alien species was about 28%. Wolff (1999) re-analyzed these data and included three more estuaries in the northern Netherlands and Germany. He found that tidal and stagnant low salinity habitats of seven Dutch and German estuaries harbored a higher proportion of alien species (about 20%) than estuarine high salinity habitats (about 6%). This pattern was not clearly related to propagule pressure (harbors and aquaculture were not focused in the middle salinity). Lee et al. (2003) found that patterns of invasion varied along an estuarine gradient in San Francisco Bay; soft-bottom benthic communities at estuarine salinities were more invaded than communities at either brackish or marine salinities. Wasson et al. (2005) found hard substrates to be more invaded than soft substrates, and a site near the mouth of an estuary to be less

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invaded than a site nearer the head of an estuary in Central California, despite the harbors in this estuary being closer to the mouth.

Few studies have made comparisons between habitats within versus outside of estuaries. Reise et al. (1999) examined benthic macroinvertebrates on the North Sea coast, and found that 6% of species were alien in coastal habitats as well as in high salinity estuarine habitats, while 20% of species in the brackish parts of estuaries were alien species. Wasson et al. (2005) found that while about 11% of the invertebrate species within a Californian estuary were alien, only 1.5% of those on the adjacent open coast were.

Understanding habitat differences in invasion rates is critical for development and implementation of management strategies (see also Chap. 7, Johnston et al.; Chap. 8, Miller and Ruiz; Chap. 12, Olyarnik et al.). As a first step, identifying those habitats that appear to be most vulnerable to establishment of alien species, and those most susceptible to major impacts from invasions is valuable for focusing prevention efforts. Second, unraveling the mechanisms behind invasion success vs failure in different habitats is critical for developing control strategies. Here we attempt to provide a global perspective on differences in invasion rates between estuaries vs adjacent open coast habitats in temperate zones, as one of many possible explorations of habitat differences in invasion rates at a broad geographic scale.

33.2 An Estuarine Emphasis to Marine Invasion Research

Traditionally, marine invasion research has been focused especially intensely on estuarine habitats. Pioneering studies were conducted in estuarine habitats, for instance by Dolgikh (1969) in the Tiligul Estuary, Ukraine and Carlton (1979) in San Francisco Bay, California. Most comprehensive recent syntheses of alien marine diversity (e.g., Cohen and Carlton 1995; Hewitt et al. 1999; Ruiz et al. 2000) focus on estuaries.

The focus on estuaries presumably stems from qualitative observations of their comparatively high invasion rates. Estuaries are often the sites of intensive human activities such as shipping and aquaculture, especially of oysters. These two human activities are considered responsible for the majority of marine introductions (Carlton 1989; Cohen et al. 1995; Carlton 1996; Ruiz et al. 1997; Reise et al. 1999; Emmett et al. 2000; Wolff 2005). Additionally, alien species may have a particularly good opportunity to become established in estuaries because low native species richness may render competition with natives weak (Elton 1958; Lodge 1993; Wolff 1973, 1999), because human alterations such as pollution and diking result in natives not being well adapted to current conditions (e.g., Byers 2002; Kennish 2002; Chap. 14, Byers), or because the semi-closed circulation of larvae allows for retention of small populations (Wasson et al. 2005). Despite these multiple explanations for high estuarine invasion rates, there has been no broad scale assessment of whether estuaries are in fact more invaded than adjacent coastal habitats. We therefore provide such an evaluation as a means to explore the above hypotheses in greater depth.

33.3 A Synthesis of Global Temperate Invertebrate Data on Invasions

33.3.1 Estuarine vs Open Coast Invasions

In order to broadly characterize estuarine vs coastal invasion rates globally, we solicited invertebrate datasets from researchers around the world. We requested data from surveys with comparable search effort in adjacent estuarine vs open coast habitats. We obtained four comprehensive invertebrate datasets (native, alien, and in some cases, cryptogenic species) and four additional datasets for only alien species, all for temperate zones (Fig. 33.1, Table 33.1). The datasets were collected for various purposes, with different sampling effort, taxonomic focus, and substrate types between regions. It would have been more desirable, of course, to have a single team consistently collect and identify specimens from all sites, using an identical protocol everywhere; such an investigation would yield sound, comprehensive results. Until such an investigation is undertaken, analysis and synthesis of data sets collected by different teams is useful for suggesting interesting preliminary trends in global invasion rates of estuaries vs coasts.

While search effort differed between coasts, search effort between estuaries vs adjacent coasts was broadly similar for each regional pairing. For the most part, similar substrate types (e.g., hard vs soft; vegetated vs unvegetated areas) and depths were searched in each regional pairing (Table 33.2). Hence, the comparisons of invasions between estuaries and open coasts appear robust. Comparisons

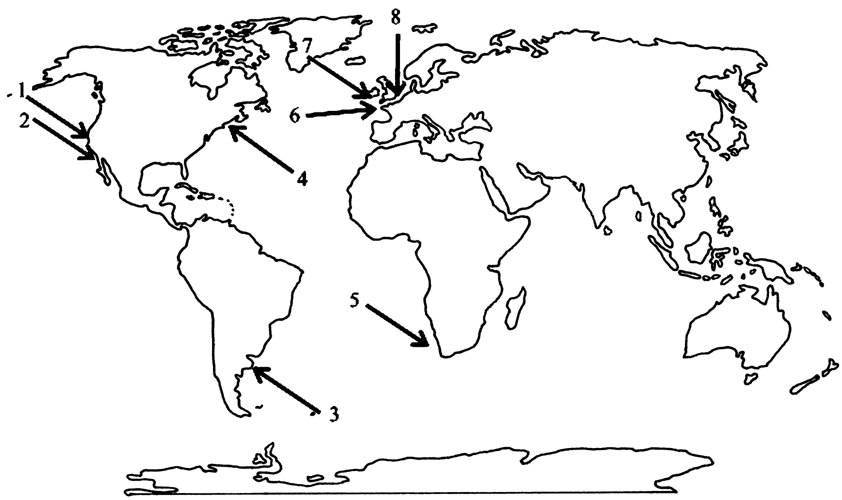

Fig. 33.1 Eight regions used for global comparison of estuarine vs coastal invertebrate invasion rates. Numbering corresponds to Table 33.1

Table 33.1 Sources of invertebrate data sets for global comparisons of habitat differences in invasion[a]

Bioregion	Location	Map	Estuarine habitat	Coastal habitat	Info on natives	Published source	Unpublished source
Northeast Pacific	Central California, USA	1	Elkhorn Slough	Rocky intertidal Carmel-Pigeon Point	yes	Wasson et al. 2001, Wasson et al. 2005	K. Wasson; J. Pearse
Northeast Pacific	Southern California, USA	2	Mission Bay	San Diego County	no	-	J. Crooks
Southwest Atlantic	Argentina	3	Mar Chiquita Coastal Lagoon	Mar del Plata	yes	-	O. Iribarne
Northwest Atlantic	New Hampshire, USA	4	Hilton Park	Odiorne State Park	yes	Tyrrell 2002	M. Tyrrell
Southeast Atlantic	South Africa	5	Langebaan Lagoon, False Bay, Knysna Estuary	Entire coast of South Africa	no	-	T. Robinson
Northeast Atlantic	France	6	Bay des Veys, Prevost Lagoon, Berre Lagoon, Bay of Morlaix, Charente Estuary	Calvados coast, Arcachon Basin, French Atlantic Coast	no	-	P. Garcia-Meunier
Northeast Atlantic	Ireland	7	Bantry Bay	Irish coast	no	-	D. Minchin
Northeast Atlantic	Netherlands	8	4 large estuaries in Delta area	Adjacent North Sea	yes	Wolff 1973	-
Northeast Atlantic	Netherlands, Germany	8	7 large estuaries in the Netherlands and Germany	High-salinity part of same estuaries	no	Wolff 1999	-

[a]The four surveys that included data for natives as well as alien species were used for the analyses summarized in Table 33.3; all studies were used for Tables 33.4 and 33.5

between regions in proportions of alien/native species are also likely sound, but comparisons of absolute numbers of alien species between regions are weaker, since search methods and effort differed. We report on trends between regions but emphasize that further studies, with consistent methods across regions, are needed for more rigorous assessments. We omitted species that are known to occur only in harbors in either habitat, thus our analysis pertains only to alien species that have established outside harbors. Finally, only established aliens were included in all databases; species that were only ever seen once, or were anecdotally reported as alien species were not included in the data sets.

For the four comprehensive datasets, we found that the percent of all invertebrates that were alien was higher, but not significantly (paired t-test, $df=3$, $p<0.203$), for estuaries (11.9%) vs coasts (7.9%) (Table 33.3). However, for three out of four of these regions, estuaries had a noticeably higher percentage of alien species than coasts (Fig. 33.2).

For all eight datasets of alien species, we found that on average 86.9% of the total number of alien species in a region occurred in estuaries whereas as only 33.2% occurred on the open coast. This result was highly significant (paired t-test, $df=7$, $p<0.006$). In six of the eight regions, there were clearly more alien species in the estuaries than on the open coasts (Fig. 33.3). For most regions, the majority of recorded alien invertebrates occurred only in estuaries, with only a few present on the coast or in both estuary and coast (Table 33.4).

Overall, our global dataset includes 198 alien invertebrates (Table 33.5). Of these, nine are found only in coastal habitats around the world, while the rest occur in estuaries (solely, or both in estuaries and on the open coast). This result provides a striking contrast. Patterns for the four major taxa included in most surveys are similar to the combined data for all taxa, but a few patterns are noteworthy. It appears that

Table 33.2 Surveyed habitats for four regions[a]

Habitat	Depth	Substrate	Northeast Pacific	Northwest Atlantic	Southwest Atlantic	Northeast Atlantic
Coast	Intertidal	Soft	No	No	Yes	Yes
		Hard	Yes	Yes	Yes	Yes
		Vegetation	No	Yes	Yes	Yes
	Subtidal	Soft	No	No	Yes	Yes
		Hard	No	No	Yes	Yes
		Vegetation	No	No	Yes	Yes
Estuary	Intertidal	Soft	Yes	No	Yes	Yes
		Hard	Yes	Yes	Yes	Yes
		Vegetation	No	Yes	Yes	Yes
	Subtidal	Soft	No	No	Yes	Yes
		Hard	No	No	Yes	Yes
		Vegetation	No	No	Yes	Yes

[a]List of habitat types, depth ranges (intertidal, subtidal), and substrate types surveyed in regions for which both alien and native species information was available

Table 33.3 Comparison of invasion rates across four regions[a]

	Estuary			Coast		
	Native	Cryptogenic	Alien	Native	Cryptogenic	Alien
North East Pacific (Central California)						
Annelids	90% (122)	6.5% (9)	3.5% (5)	99.5% (185)	0.5% (1)	0% (0)
Molluscs	91% (141)	0.5% (1)	8.5% (13)	99% (198)	0.5% (1)	0.5% (1)
Crustaceans	87% (134)	1.5% (2)	11.5% (18)	100% (79)	0% (0)	0% (0)
Bryozoans	35% (6)	24% (4)	41% (7)	87.5% (49)	7% (4)	5.5% (3)
All Taxa	84% (455)	5% (29)	11% (60)	96% (567)	2.5% (13)	1.5% (8)
North West Atlantic (New Hampshire)						
Annelids	100% (2)	0% (0)	0% (0)	100% (4)	0% (0)	0% (0)
Molluscs	91% (10)	0% (0)	9% (1)	89% (8)	0% (0)	11% (1)
Crustaceans	78% (7)	0% (0)	22% (2)	60% (3)	0% (0)	40% (2)
Bryozoans	33.3% (1)	33.3% (1)	33.3% (1)	100% (1)	0% (0)	0% (0)
All Taxa	78% (25)	3% (1)	19% (6)	79% (23)	0% (0)	21% (6)
South West Atlantic (Argentina)						
Annelids	83% (5)	0% (0)	17% (1)	100% (10)	0% (0)	0% (0)
Molluscs	100% (5)	0% (0)	0% (0)	100% (11)	0% (0)	0% (0)
Crustaceans	100% (6)	0% (0)	0% (0)	86% (12)	0% (0)	14% (2)
Bryozoans	0% (0)	0% (0)	0% (0)	100% (1)	0% (0)	0% (0)
All Taxa	89% (16)	0% (0)	11% (2)	95% (59)	0% (0)	5% (3)
North East Atlantic (Netherlands) – 1973						
Annelids	99% (79)	–	1% (1)	98% (51)	–	2% (1)
Molluscs	89% (56)	–	11% (7)	96% (25)	–	4% (1)
Crustaceans	91% (60)	–	9% (6)	91% (31)	–	9% (3)
–	–	–	–	–	–	–
All Taxa	93% (195)	–	7% (14)	96% (107)	–	4% (5)

[a]Percent (and absolute number in parentheses) of total invertebrate species that were native, cryptogenic and alien are shown for adjacent estuarine and open coast habitats, for four taxa surveyed in most studies and for all taxa combined

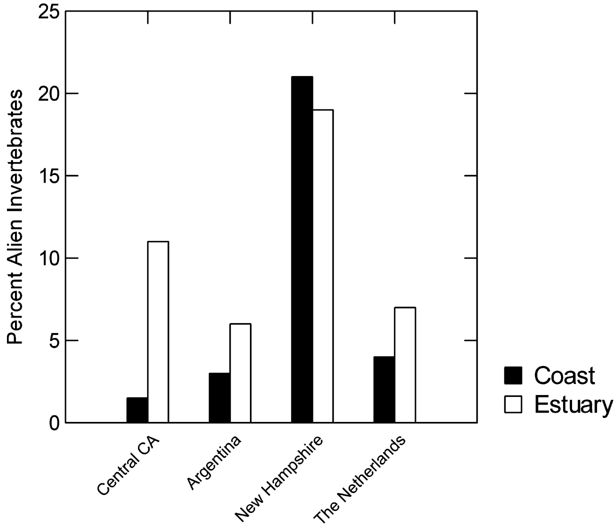

Fig. 33.2 Percent of total documented invertebrate species that were alien, in coastal vs estuarine habitats in four regions

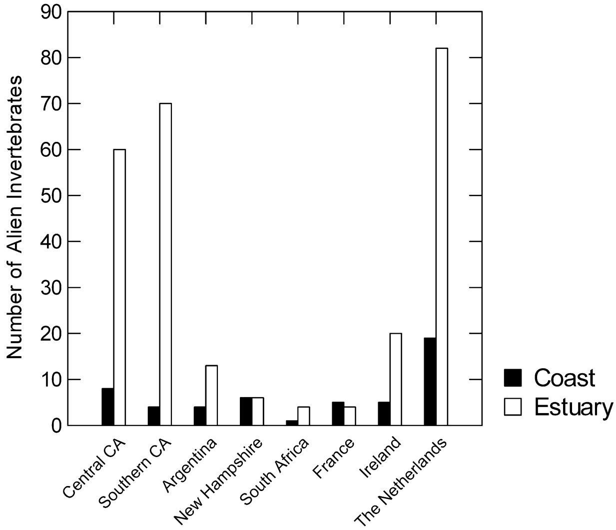

Fig. 33.3 Number of alien invertebrate species that were found in coastal vs estuarine habitats in eight regions

Table 33.4 Comparison of habitat associations of alien species across eight regions[a]

Taxon	Estuary only	Estuary & Coast	Coast only
Northeast Pacific (Central California)			
Annelids	100% (5)	0% (0)	0% (0)
Molluscs	93% (14)	7% (1)	0% (0)
Crustaceans	100% (17)	0% (0)	0% (0)
Bryozoans	63% (5)	37% (3)	0% (0)
All taxa	87% (52)	13% (8)	0% (0)
Northeast Pacific (Southern California, San Diego)			
Annelids	100% (11)	0% (0)	0% (0)
Molluscs	56% (5)	33% (3)	11% (1)
Crustaceans	100% (24)	0% (0)	0% (0)
Bryozoans	100% (6)	0% (0)	0% (0)
All Taxa	94% (66)	4% (3)	2% (1)
Southwest Atlantic (South America, Argentina)			
Annelids	0% (0)	100% (2)	0% (0)
Molluscs	100% (3)	0% (0)	0% (0)
Crustaceans	67% (4)	0% (0)	33% (2)
Bryozoans	0% (0)	0% (0)	0% (0)
All Taxa	73.3% (11)	13.3% (2)	13.3% (2)
Northwest Atlantic (New Hampshire)			
Annelids	0% (0)	0% (0)	0% (0)
Molluscs	0% (0)	100% (1)	0% (0)
Crustaceans	0% (0)	100% (2)	0% (0)
Bryozoans	0% (0)	100% (1)	0% (0)
All Taxa	0% (0)	100% (6)	0% (0)

(continued)

Table 33.4 (continued)

Taxon	Estuary only	Estuary & Coast	Coast only
Northeast Atlantic (Ireland)			
Annelids	100% (1)	0% (0)	0% (0)
Molluscs	86% (6)	14% (1)	0% (0)
Crustaceans	80% (8)	10% (1)	10% (1)
Bryozoans	0% (0)	0% (0)	0% (0)
All taxa	77% (17)	14% (3)	9% (2)
Northeast Atlantic (Netherlands)			
Annelids	86% (12)	7% (1)	7% (1)
Molluscs	70% (14)	25% (5)	5% (1)
Crustaceans	62% (16)	27% (7)	11% (3)
Bryozoans	100% (7)	0% (0)	0% (0)
All Taxa	78% (68)	16% (14)	6% (5)
Northeast Atlantic (France)			
Annelids	25% (1)	0% (0)	75% (3)
Molluscs	33% (1)	0% (0)	67% (2)
Crustaceans	100% (2)	0% (0)	0% (0)
Bryozoans	0% (0)	0% (0)	0% (0)
All Taxa	44% (4)	0% (0)	56% (5)
Southeast Atlantic (South Africa)			
Annelids	0% (0)	0% (0)	0% (0)
Molluscs	67% (2)	0% (0)	33% (1)
Crustaceans	100% (1)	0% (0)	0% (0)
Bryozoans	0% (0)	0% (0)	0% (0)
All Taxa	80% (4)	0% (0)	20% (1)

[a]Percent (and absolute number in parentheses) of alien species that were found only in estuaries, in both estuary and coast, or only on the open coast are shown for four taxa surveyed in most studies and for all taxa combined

bryozoans are almost exclusively invaders of estuarine, not coastal habitats. Of the four data sets that provided data on all types of species, a minority of the estuarine bryozoan species present are native (Table 33.3), and almost all reported alien bryozoans occur in estuaries (Tables 33.4 and 33.5). In contrast, crustaceans are the most common invaders of coastal habitats (Tables 33.4 and 33.5). Although we only synthesized invertebrate data in this study, greater numbers of estuarine vs coastal aliens have also been noted for algae (Wolff 2005, for the Netherlands) and fish (Crooks, personal communication, for southern California).

33.3.2 Regional Differences in Estuarine vs Coastal Invasions

Examination of our global comparison of estuarine vs coastal invertebrate invasions reveals striking regional differences (Table 33.3). Of course, these differences may in part be due to differences in search effort or sampling method, because these

Table 33.5 Alien species reported from eight regions[a–e]

	Northeast Pacific		South West Atlantic	North West Atlantic	Northeast Atlantic			South East Atlantic			
Species / Region	Central California	Southern California	Argentina	New Hampshire	Ireland	Netherlands	France	South Africa	# of regions that species is found in	Estuarine records	Coastal records
PORIFERA	-	-	-	-	-	-	-	-	-	-	-
Cliona celata var. lobata	C, E	-	-	-	-	-	-	-	1	1	1
Halichondria bowerbanki	C, E	-	-	-	-	-	-	-	1	1	1
Haliclona loosanoffi	E	-	-	-	-	E	-	-	2	2	0
Haliclona rosea	-	-	-	-	-	E	-	-	1	1	0
Haliclona cf. simplex	-	-	-	-	-	E	-	-	1	1	0
Hymeniacidon perlevis	-	-	-	-	-	E	-	-	1	1	0
Hymeniacidon sinapium	C, E	-	-	-	-	-	-	-	1	1	1
Mycale micracanthoxea	-	-	-	-	-	E	-	-	1	1	0
Scypha scaldiensis	-	-	-	-	-	E	-	-	1	1	0
CNIDARIA	-	-	-	-	-	-	-	-	-	-	-
HYDROZOA	-	-	-	-	-	-	-	-	-	-	-
Clavopsella navis	-	-	-	-	-	E	-	-	1	1	0
Cordylophora caspia	E	-	-	-	-	E	-	-	2	2	0
Ectopleura crocea	E	E	-	-	-	-	-	-	2	2	0
Garveia franciscana	-	-	-	-	-	E	-	-	1	1	0
Gonionemus vertens	-	-	-	-	-	E	-	-	1	1	0
Nemopsis bachei	-	-	-	-	-	E	-	-	1	1	0
Sarsia tubulosa	E	-	-	-	-	-	-	-	1	1	0
Ostroumovia inkermanica	-	-	-	-	-	E	-	-	1	1	0
Thieliana navis	-	-	-	-	-	E	-	-	1	1	0
ANTHOZOA	-	-	-	-	-	-	-	-	-	-	-
Bunodeopsis sp.	-	E	-	-	-	-	-	-	1	1	0

(continued)

Table 33.5 (continued)

	Northeast Pacific		South West Atlantic	North West Atlantic	Northeast Atlantic			South East Atlantic			
Species / Region	Central California	Southern California	Argentina	New Hampshire	Ireland	Netherlands	France	South Africa	# of regions that species is found in	Estuarine records	Coastal records
Diadumene cincta	-	-	-	-	-	C, E	-	-	1	1	1
Diadumene franciscana	E	E	-	-	-	-	-	-	2	2	0
Diadumene leucolena	E	-	-	-	-	-	-	-	1	1	0
Diadumene lineata	E	E	-	C, E	E	E	-	-	5	5	1
NEMATODA	-	-	-	-	-	-	-	-	-	-	-
Anguillicola crassus	-	-	-	-	C, E	E	-	-	2	2	1
PLATYHELMINTHES	-	-	-	-	-	-	-	-	-	-	-
TREMATODA	-	-	-	-	-	-	-	-	-	-	-
Cercaria batillariae	E	-	-	-	-	-	-	-	1	1	0
TURBELLARIA	-	-	-	-	-	-	-	-	-	-	-
Euplana gracilis	-	-	-	-	-	E	-	-	1	1	0
Stylochus flevensis	-	-	-	-	-	E	-	-	1	1	0
ANNELIDS	-	-	-	-	-	-	-	-	-	-	-
OLIGOCHAETES	-	-	-	-	-	-	-	-	-	-	-
Tubificoides brownea	-	E	-	-	-	-	-	-	1	1	0
Tubificoides heterochaetus	-	-	-	-	-	E	-	-	1	1	0
POLYCHAETA	-	-	-	-	-	-	-	-	-	-	-
Amblyosyllis speciosa	-	E	-	-	-	-	-	-	1	1	0
Aphelochaeta marioni	-	-	-	-	-	E	-	-	1	1	0
Boccardia ligerica	-	-	C, E	-	-	-	-	-	1	1	1
Boccardia polybranchia	-	-	-	-	-	-	C	-	1	0	1
Boccardia semibranchiata	-	-	-	-	-	-	E	-	1	1	0
Clymenella torquata	-	-	-	-	-	E	-	-	1	1	0
Demonax sp.	-	E	-	-	-	-	-	-	1	1	0

Ficopomatus enigmaticus	E	-	C, E	-	E	E	-	-	4	4	1
Heteromastus filiformis	E	-	-	-	-	-	-	-	1	1	0
Hydroides dirampa	-	E	-	-	-	-	-	-	1	1	0
Hydroides elegans	-	E	-	-	-	E	-	-	2	2	0
Janua brasiliensis	-	-	-	-	-	E	-	-	1	1	0
Lycatopsis pontica	-	E	-	-	-	-	-	-	1	1	0
Marenzelleria cf. wireni	-	-	-	-	-	E	-	-	1	1	0
Microphthalmus similis	-	-	-	-	-	C	-	-	1	0	1
Myrianida pachycera	-	E	-	-	-	-	-	-	1	1	0
Neanthes acuminata	-	E	-	-	-	-	-	-	1	1	0
Nereis virens	-	-	-	-	-	E	-	-	1	1	0
Nicolea sp. A	-	E	-	-	-	-	-	-	1	1	0
Polydora ciliata	-	-	-	-	-	-	C	-	1	0	1
Polydora hoplura	-	-	-	-	-	E	C	-	2	1	1
Polydora cornuta	E	-	-	-	-	-	-	-	1	1	0
Proceraea cornuta	-	-	-	-	-	E	-	-	1	1	0
Pseudopolydora paucibranchiata	E	E	-	-	-	-	-	-	2	2	0
Sabellaria spinulosa	-	-	-	-	-	C, E	-	-	1	1	1
Streblospio benedicti	E	E	-	-	-	-	-	-	2	2	0
MOLLUSCA	-	-	-	-	-	-	-	-	-	-	-
POLYPLACOPHORA	-	-	-	-	-	-	-	-	-	-	-
Lepidopleurus cancellatus	-	-	-	-	-	C, E	-	-	1	1	1
GASTROPODS	-	-	-	-	-	-	-	-	-	-	-
Aoelidella takanosimensis	-	C, E	-	-	-	-	-	-	1	1	1
Babakina festiva	-	E	-	-	-	-	-	-	1	1	0
Batillaria attramentaria	E	-	-	-	-	-	-	-	1	1	0
Callistoma zizyphinum	-	-	-	-	-	E	-	-	1	1	0
Calyptraea chinensis	-	-	-	-	E	E	-	-	2	2	0
Catriona rickettsi	-	C, E	-	-	-	-	-	-	1	1	1
Corambe batava	-	-	-	-	-	E	-	-	1	1	0

(continued)

Table 33.5 (continued)

	Northeast Pacific		South West Atlantic	North West Atlantic	Northeast Atlantic			South East Atlantic			
Species / **Region**	Central California	Southern California	Argentina	New Hampshire	Ireland	Netherlands	France	South Africa	# of regions that species is found in	Estuarine records	Coastal records
Crepidula fornicata	-	-	-	-	E	C, E	C	-	3	2	2
Cyclope neritea	-	-	-	-	-	-	E	-	1	1	0
Gibbula cineraria	-	-	-	-	-	E	-	-	1	1	0
Littorina littorea	-	-	-	C, E	-	-	-	-	1	1	1
Littorina saxatilis	-	-	-	-	-	-	-	E	1	1	0
Myosotella myosotis	E	-	-	-	-	-	-	-	1	1	0
Ocenebra erinacea	-	-	-	-	-	E	-	-	1	1	0
Okenia plana	E	-	-	-	-	-	-	-	1	1	0
Philine auriformis	E	C	-	-	-	-	-	-	2	1	1
Potamopyrgus antipodarum	-	-	-	-	E	E	-	-	2	2	0
Rapana venosa	-	-	E	-	-	-	C	-	2	1	1
Tenellia adspersa	E	-	-	-	-	-	-	-	1	1	0
Urosalpinx cinerea	E	-	-	-	-	E	-	-	2	2	0
BIVALVIA	-	-	-	-	-	-	-	-	-	-	-
Corbicula fluminalis	-	-	-	-	-	E	-	-	1	1	0
Crassostrea gigas	E	E	E	-	E	E	-	E	6	6	0
Crassostrea virginica	E	-	-	-	-	-	-	-	1	1	0
Dreissena polymorpha	-	-	-	-	-	E	-	-	1	1	0
Ensis directus	-	-	-	-	-	C, E	-	-	1	1	1
Gemma gemma	E	-	-	-	-	-	-	-	1	1	0
Limnoperna fortunei	-	-	E	-	-	-	-	-	1	1	0
Mercenaria mercenaria	-	?	-	-	-	E	-	-	2	1	0
Musculista senhousia	E	E	-	-	-	-	-	-	2	2	0
Mytilopsis leucophaeata	-	-	-	-	-	E	-	-	1	1	0

Mytilus galloprovincialis	C, E	C, E	-	-	-	-	-	C	3	2	3
Mya arenaria	E	-	-	-	E	E	-	-	3	3	0
Nutallia obscurata	E	-	-	-	-	-	-	-	1	1	0
Lyrodus pedicellatus	E	E	-	-	-	-	-	-	2	2	0
Petricola pholadiformis	-	-	-	-	-	C, E	-	-	1	1	1
Psiloteredo megotara	-	-	-	-	-	C	-	-	1	0	1
Ruditapes semidecussata	-	-	-	-	E	-	-	-	1	1	0
Spisula solidissima	-	-	-	-	-	E	-	-	1	1	0
Teredo navalis	-	-	-	-	C, E	C, E	-	-	2	2	2
Theora fragilis	-	E	-	-	-	-	-	-	1	1	0
Venerupis philippinarum	E	-	-	-	-	-	?	-	2	1	0
BRYOZOA	-	-	-	-	-	-	-	-	-	-	-
Alcyonidium polyoum	-	-	-	C, E	-	-	-	-	1	1	1
Amathia vidovici	E	-	-	-	-	-	-	-	1	1	0
Bowerbankia gracilis	E	E	-	-	-	E	-	-	3	3	0
Bowerbankia imbricata	-	-	-	-	-	E	-	-	1	1	0
Bugula neritina	C, E	E	-	-	-	?	-	-	3	2	1
Bugula simplex	-	-	-	-	-	E	-	-	1	1	0
Bugula stolonifera	E	-	-	-	-	E	-	-	2	2	0
Conopeum tenuissimum	E	-	-	-	-	-	-	-	1	1	0
Cryptosula pallasiana	C, E	E	-	-	-	-	-	-	2	2	1
Schizoporella unicornis	C, E	-	-	-	-	-	-	-	1	1	1
Tricellaria inopinata	-	-	-	-	-	E	-	-	1	1	0
Victoriella pavida	-	-	-	-	-	E	-	-	1	1	0
Walkeria uva	-	-	-	-	-	E	-	-	1	1	0
Watersipora arcuata	-	E	-	-	-	-	-	-	1	1	0
Watersipora subtorquata	E	E	-	-	-	-	-	-	2	2	0
Zoobotryon verticillatum	-	E	-	-	-	-	-	-	1	1	0
KAMPTOZOA	-	-	-	-	-	-	-	-	-	-	-
Barentsia benedeni	E	-	-	-	-	-	-	-	1	1	0

(continued)

Table 33.5 (continued)

Species / Region	Northeast Pacific		South West Atlantic	North West Atlantic	Northeast Atlantic			South East Atlantic			
	Central California	Southern California	Argentina	New Hampshire	Ireland	Netherlands	France	South Africa	# of regions that species is found in	Estuarine records	Coastal records
CRUSTACEA	-	-	-	-	-	-	-	-	-	-	-
AMPHIPODA	-	-	-	-	-	-	-	-	-	-	-
Ampithoe valida	E	-	-	-	-	-	-	-	1	1	0
Aoroides secunda	-	E	-	-	-	-	-	-	1	1	0
Caprella mutica	E	-	-	-	C	E	-	-	3	2	1
Chelicorophium curvispinum	-	-	-	-	-	E	-	-	1	1	0
Chelura terebrans	-	-	-	-	-	-	-	E	1	1	0
Corophium acherusicum	E	E	-	-	-	-	-	-	2	2	0
Corophium heteroceratum	-	E	-	-	-	-	-	-	1	1	0
Elasmopus rapax	-	E	-	-	-	-	-	-	1	1	0
Ericthonius brasiliensis	-	E	-	-	-	-	-	-	1	1	0
Gammarus tigrinus	-	-	-	-	-	E	-	-	1	1	0
Grandidierella japonica	E	E	-	-	-	-	-	-	2	2	0
Incisocalliope aestuarius	-	-	-	-	-	E	-	-	1	1	0
Jassa marmorata	E	E	-	-	-	-	-	-	2	2	0
Leucothoe alata	-	E	-	-	-	-	-	-	1	1	0
Liljeborgia sp.	-	E	-	-	-	-	-	-	1	1	0
Melita nitida	E	-	-	-	-	E	-	-	2	2	0
Monocorophium insidiosum	E	E	E	-	-	-	-	-	3	3	0
Monocorophium uenoi	E	E	-	-	-	-	-	-	2	2	0
Orchestia cavimana	-	-	-	-	-	E	-	-	1	1	0
Parapleustes derzhavini	E	-	-	-	-	-	-	-	1	1	0
Platorchestia platensis	-	-	-	-	-	E	-	-	1	1	0
Stenothoe valida	-	E	-	-	-	-	-	-	1	1	0

CIRRIPEDIA	-	-	-	-	-	-	-	-	-	-	-
Balanus amphitrite	-	E	E	-	-	C, E	-	-	3	3	1
Balanus balanus	-	-	-	-	-	C, E	-	-	1	1	1
Balanus eburneus	-	-	-	-	-	E	-	-	1	1	0
Balanus glandula	-	-	C	-	-	-	-	-	1	0	1
Balanus improvisus	E	-	-	-	E	C, E	-	-	3	3	1
Elminius modestus	-	-	-	-	C, E	C, E	-	-	2	2	2
Megabalanus coccopoma	-	-	-	-	-	C	-	-	1	0	1
Megabalanus tintinnabulum	-	-	-	-	-	C	-	-	1	0	1
COPEPODA	-	-	-	-	-	-	-	-	-	-	-
Acartia tonsa	-	-	-	-	-	E	-	-	1	1	0
Eurytemora americana	-	-	-	-	-	E	-	-	1	1	0
Herrmannella duggani	-	-	-	-	E	-	-	-	1	1	0
Myicola ostreae	-	-	-	-	E	E	-	-	2	2	0
Mytilicola intestinalis	-	-	-	-	E	E	-	-	2	2	0
Mytilicola orientalis	E	-	-	-	E	E	-	-	3	3	0
Pseudodiaptomus marinus	-	E	-	-	-	-	-	-	1	1	0
DECAPODA	-	-	-	-	-	-	-	-	-	-	-
Eriocheir sinensis	-	-	-	-	-	C, E	E	-	2	2	1
Callinectes sapidus	-	-	-	-	-	C, E	E	-	2	2	1
Carcinus maenas	E	-	-	C, E	-	-	-	?	3	2	1
Hemigrapsus penicillatus	-	-	-	-	-	E	-	-	1	1	0
Hemigrapsus sanguineus	-	-	-	C, E	-	C, E	-	-	2	2	2
Palaemon macrodactylus	E	E	-	-	-	-	-	-	2	2	0
Pyromaia tuberculata	-	-	?	-	-	-	-	-	1	0	0
Rhithropanopeus harrisii	-	-	-	-	-	E	-	-	1	1	0
ISOPODA	-	-	-	-	-	-	-	-	-	-	-
Halophiloscia couchii	-	-	?	-	-	-	-	-	1	0	0
Iais californica	E	E	-	-	-	-	-	-	2	2	0
Idotea baltica	-	-	C	-	-	-	-	-	1	0	1
Idotea metallica	-	-	E	-	-	-	-	-	1	1	0
Ligia exotica	-	-	E	-	-	-	-	-	1	1	0

(continued)

Table 33.5 (continued)

	Northeast Pacific		South West Atlantic	North West Atlantic	Northeast Atlantic			South East Atlantic			
Species / **Region**	Central California	Southern California	Argentina	New Hampshire	Ireland	Netherlands	France	South Africa	# of regions that species is found in	Estuarine records	Coastal records
Limnoria quadripunctata	E	E	-	-	-	C	-	-	3	2	1
Limnoria tripunctata	-	E	-	-	E	-	-	-	2	2	0
Paranthura japonica	-	E	-	-	-	-	-	-	1	1	0
Porcellanum ovatum	-	-	-	-	E	-	-	-	1	1	0
Sphaeroma quoyanum	E	E	-	-	-	-	-	-	2	2	0
Sphaeroma serratum	-	-	?	-	-	-	-	-	1	0	0
Sphaeroma walkeri	-	E	-	-	-	-	-	-	1	1	0
Synidotea laevidorsalis	-	-	?	-	-	-	-	-	1	0	0
MYSIDACEA	-	-	-	-	-	-	-	-	-	-	-
Hemimysis anomala	-	-	-	-	-	E	-	-	1	1	0
OSTRACODA	-	-	-	-	-	-	-	-	-	-	-
Aspidoconcha limnoriae	-	E	-	-	-	-	-	-	1	1	0
Redekea californica	-	E	-	-	-	-	-	-	1	1	0
TANAICIDAE	-	-	-	-	-	-	-	-	-	-	-
Sinelobus	E	-	-	-	-	-	-	-	1	1	0
Sinelobus? stanfordi	-	E	-	-	-	-	-	-	1	1	0
UROCHORDATA	-	-	-	-	-	-	-	-	-	-	-
Aplidium glabrum	-	-	-	-	-	E	-	-	1	1	0
Ascidia sp.	-	E	-	-	-	-	-	-	1	1	0
Ascidia zara	-	E	-	-	-	-	-	-	1	1	0
Bostrichobranchus pilularis	-	E	-	-	-	-	-	-	1	1	0
Botryllus schlosseri	-	E	E	-	-	-	-	-	2	2	0
Botryllus firmus	-	E	-	-	-	-	-	-	1	1	0
Botryllus sp. A	-	E	-	-	-	-	-	-	1	1	0

Botrylloides violaceus	E	E	-	C, E	-	E	-	-	4	4	1
Ciona intestinalis	-	E	E	-	-	-	-	-	2	2	0
Ciona robusta	-	-	E	-	-	-	-	-	1	1	0
Ciona savigny	-	E	-	-	-	-	-	-	1	1	0
Clavelina lapadiformis	-	-	-	-	-	-	-	E	1	1	0
Diplosoma listerianusm	-	-	-	-	-	E	-	-	1	1	0
Microcosmus squamiger	-	E	-	-	-	-	-	-	1	1	0
Molgula manhattensis	C, E	-	E	-	-	E	-	-	3	3	1
Phallusia mammilata	-	-	-	-	C	-	-	-	1	0	1
Polyandrocarpa zorritensis	-	E	-	-	-	-	-	-	1	1	0
Styela canopus	-	E	-	-	-	-	-	-	1	1	0
Styela clava	E	E	-	-	E	E	-	-	4	4	0
Styela plicata	-	E	-	-	-	-	-	-	1	1	0
Symplegma brakenhelmi	-	E	-	-	-	-	-	-	1	1	0
Symplegma reptans	-	E	-	-	-	-	-	-	1	1	0

[a]Species found in three or more localities listed in dark gray shading
[b]Species found only in coastal habitats listed in light gray shading
[c]Species whose habitat association is unknown marked with "?"
[d]'C' means that a species is found on an open coast
[e]'E' means that a species is found in an estuary

were not consistent across regions. We suspect, however, that at least the most pronounced differences are real.

For the four comprehensive datasets, we found that the difference between coast and estuary was most dramatic in California, where 1.5% of documented coastal invertebrates vs 11% of estuarine invertebrates were alien (Table 33.3). The same trend of lower percentage of aliens in coastal vs estuarine habitats was present in Argentina (5% vs 11%, for a very low sample size) and the Netherlands (4% vs 7%), but much less pronounced (mostly due to higher coastal invasion rates). In New Hampshire, coastal and estuarine habitats had similar percentages of aliens (21% vs 19%), much higher in both habitats than in the other regions. Survey methods differed between regions, with those in California and the Netherlands representing extensive searches over many years, while those for Argentina and New Hampshire consisted of more focused, shorter efforts. (A more focused, short-term survey at the same estuary in California detected only 47 total species, with aliens representing 21% of species in soft substrates, 52% on hard substrates – much higher than the 11% overall level calculated when every native species ever reported for the estuary is included in the analysis; Wasson et al. 2005). Nevertheless, we suspect that the general pattern – no difference in estuarine vs coastal invasion rates in New Hampshire, vs marked differences in the other three regions (Fig. 33.2) – is real and will be borne out by more consistently designed future comparisons.

In the comparison of habitat associations of alien species from eight regions, strong differences also emerged. In six regions (Central and Southern California, Argentina, South Africa, Ireland, and the Netherlands), there was a markedly higher number of alien species documented from estuarine vs coastal habitats (Fig. 33.3) – more than 70% of aliens from these regions were reported exclusively in estuaries (Table 33.4). In two regions (New Hampshire and France), numbers of alien species in estuaries vs coasts were similar (and in both cases low). Detailed patterns for these latter two differed: in New Hampshire, the six documented aliens all occurred in *both* estuarine and coastal habitats, while in France, none of the species occurred in both habitats (four aliens were found only in the estuary, and five only on the coast).

Not only did habitat associations of aliens differ among the eight regions, but also the absolute number of aliens recorded from each region (Table 33.4 and Fig. 33.3). California and the Netherlands have many more documented aliens (60 or more) than the other regions (which have 4–22 alien species). This result may simply reflect greater search effort, and should be compared to findings of other biogeographic syntheses (see also Chap. 2, Carlton).

Our compilation of alien species (Table 33.5) also reveals that 18 species are common invaders, shared across at least 3 regions. These are well-known aliens reported in other major syntheses of global invasions (Ruiz et al. 2000). None of these common invaders occurs only in coastal habitats – this cosmopolitan suite of aliens is mostly comprised of estuarine specialists, and some broadly tolerant species found in estuaries and on the coast.

33.4 Hypotheses for Higher Invasion Rates of Estuaries vs Coasts

What mechanisms are behind the higher number of aliens in estuaries vs adjacent open coast settings in most regions? We present five broad hypotheses for this phenomenon, and consider whether the patterns that emerge from our global analysis support them. We also draw on selected examples from other studies that support each hypothesis, and formulate examples of predictions that could be rigorously tested in future studies to determine the relative importance of each hypothesis for particular taxa or regions.

Differences in number of aliens in coastal vs estuarine habitats could stem both from differences in numbers of individuals introduced (propagule pressure) and from differences in establishment rates following introduction (Chap. 7, Johnston et al.; Chap.12 , Olyarnik et al.). The first hypothesis explores the former, and the remaining four hypotheses involve the latter. For establishment success, the mechanism could involve physical conditions (our second and third hypotheses) or biological interactions (our fourth and fifth ones). For a particular alien species' distribution in one region, a single mechanism may explain most of the pattern.

33.4.1 Greater Alien Propagule Pressure in Estuaries

33.4.1.1 Hypothesis

Estuaries are more invaded than adjacent coastal habitats because estuaries are subject to greater alien propagule pressure.

33.4.1.2 General Explanation

Because the two vectors considered responsible for the greatest number of marine introductions, shipping and oyster culture, are generally located in estuaries, it seems likely that many more alien species are transported among estuaries than open coast environments. This hypothesis has long been raised in the literature, and continues to be frequently invoked (e.g., Carlton 1979, 1985; Carlton and Geller 1993; Campbell and Hewitt 1999; Reise et al. 1999; Ruiz et al. 2000; Minchin and Eno 2002). Not only does it seem likely that more species are transported from estuarine than from coastal environments, it is also plausible that a greater proportion of estuarine species survive transport than do coastal ones. Conditions in ballast water tanks or in oyster transport from one aquaculture hub to another may involve fluctuating temperature and salinity conditions that broadly tolerant estuarine species are better adapted to than their coastal counterparts (Wolff 1999). Both higher transport rate and higher survival during transport would contribute to greater numbers of aliens in estuaries than coasts, given similar establishment rates following introduction.

33.4.1.3 Support from the Global Analysis

Overall, only nine alien species, a tiny fraction of the total, occurred exclusively on the coast (Table 33.5). In contrast, 37 species were found in both coastal and estuarine settings. There is no reason to expect that species that can tolerate estuarine conditions should be better at establishing on the coast than purely coastal species, so the contrast (37 mixed occurrence vs 9 purely coastal occurrences) seems likely due to greater propagule pressure in estuaries (and subsequent spread of these species from estuaries to coasts).

The contrast we report between US coasts, where similar numbers of aliens are found on the open coast but far more are found in the Pacific than Atlantic estuary, could also in part be due to the above explanation. For instance, while Elkhorn Slough (California) and Great Bay (New Hampshire) both have regular small boat traffic, only the former has a long history of alien oyster culturing, which is considered responsible for many of the introductions in Elkhorn Slough (Wasson et al. 2001). Thus, the low number of aliens on both the New Hampshire coast and estuary relative to other regions may be due, at least in part, to lower numbers of introductions.

33.4.1.4 Support from Other Observations

The highest number of alien species recorded for any one place is from an estuary, San Francisco Bay, no doubt in part due to high propagule pressure in this major shipping and former oyster culturing center (Cohen and Carlton 1998). One species-level example of propagule pressure being a key predictor of invasion patterns is the Asian mud snail *Batillaria attramentaria,* found on the US Pacific coast only in bays and estuaries where Asian oysters were cultured (Byers 1999). In this case, there appears to be a perfect correspondence of human introduction and invasion patterns (although if this mudflat species had been introduced to the open coast, it would probably not have survived, so the hypothesis in the following section would also be applicable). However, there are contrasting examples from this region. The European green crab *Carcinus maenas*, a coastal and estuarine species in its home and some introduced (e.g., US Atlantic coast) ranges is found only in estuaries along the US Pacific coast (Cohen et al. 1995). Its recent spread in this region was most likely due to larval transport on oceanic currents (Grosholz and Ruiz 1995), so propagule pressure should have been comparable in estuarine and coastal habitats along the hundreds of miles of coast where larvae have spread. Its absence from the open coast is very likely to be attributed to one of the other hypotheses described below, rather than due to introduction mechanisms.

33.4.1.5 Testable Predictions

If propagule pressure alone explains much of the variation in observed numbers of established aliens, then areas with comparable propagule pressure should have comparable numbers of established aliens. One fruitful comparison might be of small shipping harbors with comparable boat traffic along the open coast vs those in small estuaries, in a region not exposed to other vectors (no ballast water or oyster culturing). Given these constraints, the introduction mechanisms (small vessels transporting mostly hull-fouling organisms) and rates should be the similar between habitats. If numbers of established aliens (collected on settlement plates for example) are comparable in these paired coastal and estuarine harbors, it would provide support for the hypothesis that propagule pressure alone explains most of the variation in alien species richness. If, however, numbers of alien species are higher in the estuary, one of the subsequent hypotheses regarding post-introduction success must be invoked.

Another tactic is to examine the identity and number of established alien species in as opposed to near harbors from a survey as described above. If propagule pressure were the key predictor of invasion success, then we would expect an equal proportion of the alien species present to be established in natural habitats a short distance (e.g., 0.5 km) outside of harbors in both estuarine and coastal habitats. Anecdotally (Wasson, unpublished data), this does not seem to be the case for Central California – almost none of the few dozen alien invertebrates common in open coast harbors have established on the open coast. Data of this sort rigorously collected for multiple regions would refute the hypothesis that propagule pressure alone explains high estuarine invasion rates.

33.4.2 Estuarine Species are Better Suited to Estuarine Conditions

33.4.2.1 Hypothesis

Estuaries are more invaded than adjacent coastal habitats because the species that are transported between regions are typically adapted to estuarine conditions, and more likely to spread and establish within the new region in estuarine vs open coast habitats.

33.4.2.2 General Explanation

If, as postulated in the first hypothesis, more species are moved from estuary to estuary (by shipping and oyster culture in particular) than from open coast to open coast, then the identity of the species that are transported should also differ. Species that were transported from an estuary are likely to have adaptations for the physical and biological conditions of estuaries rather than open coast environments, and the transported species are therefore more likely to successfully establish in estuaries than on the open coast. This is a rather obvious observation that is simply a correlate of the first explanation. However, we raise it as a separate hypothesis because the predictions are somewhat different. The first explanation invokes high propagule pressure as the cause of high estuarine invasion rates, while this hypothesis attributes the difference in alien species numbers to higher establishment rates in estuarine vs open coast habitats following arrival, due to better matching between physical conditions in a species' native and invaded ranges. This applies both to initial establishment at the first site in a new region, and moreover to subsequent spread within a region.

33.4.2.3 Support from Global Analysis

The above logic would suggest that in regions where estuarine and coastal conditions are more similar, more alien species (largely transported from estuary to estuary) would establish on the open coast, while in regions where conditions contrast more sharply, aliens would fail to establish on the open coast. This might explain some of the difference we observed in coastal invasion rates between the Pacific and Atlantic coasts of the US. On the Pacific coast of California, high wave action may be intolerable for most estuarine species, which could account for the absence of all but 8 of the 60 species found in the estuary. On the Atlantic coast in the Gulf of Maine, wave action is much lower; thereby potentially lowering this barrier to invasion by estuarine species – and the six aliens reported from the estuary also occur on the open coast.

33.4.2.4 Support from Other Observations

Invasion rates vary along an estuarine gradient. Near the mouth, where conditions are most similar to those in adjacent marine habitats, the percentage of established aliens appears to be lower than near the head, where conditions are truly estuarine, fluctuating greatly in salinity and temperature, both daily and seasonally (Carlton 1979; Wolff 1999; Cohen and Carlton 1995; Wasson et al. 2005). In addition to salinity, water movement may also be a predictor of invasion success. In Central California (Wasson, personal observation) and New Hampshire (Tyrrell, personal observation), adjacent estuarine sites with high current speeds are far less invaded than those with slow currents. These observations of higher numbers of established aliens in more typically estuarine conditions (i.e., less water exchange, highly variable salinities) support this explanation, but are also consistent with hypotheses 33.4.3.1 and 33.4.5.1 below.

33.4.2.5 Testable Predictions

Many species arrive to a new region by one mechanism (e.g., ballast water transport), and then are secondarily transported to sites within this new region by other mechanisms (e.g., small boat traffic or natural larval transport) (Wasson et al. 2001). For such a species, secondary introduction rates to estuarine and open coast harbors should be similar following initial introduction to a region. However, if this hypothesis is supported, establishment rates should be lower in open coast harbors, because of poor matching of physical conditions under which the alien evolved. (Failure at establishment could also be due to interactions with natives or other previously introduced species, explanations 33.4.4.2 and 33.4.5.2 below, but this seems less likely in artificial harbor habitats than in natural settings.)

33.4.3 Establishment is Facilitated by the Limited Circulation in Estuaries

33.4.3.1 Hypothesis

Estuaries are more invaded than adjacent coastal habitats because they represent relatively closed systems in which small numbers of introduced individuals can more readily establish breeding populations than on the open coast.

33.4.3.2 General Explanation

Since it is probably common for only a few individuals of an alien species to be introduced in one event, establishment of an alien is unlikely if larvae or adults disperse too widely to allow for subsequent successful mating. Estuarine tidal circulation is more limited than that on the open coast, and reduced risk of gamete and larval dilution might facilitate establishment of a population from a small number of individuals in estuaries (J. Byers, personal communication; Wasson et al. 2005).

33.4.3.3 Support

None that we know of, from our data set or other observations.

33.4.3.4 Testable Predictions

This explanation should only apply to species with a long-distance dispersal stage. Therefore, a strong test of this hypothesis would be to compare estuarine vs coastal invasion rates by species with a mobile dispersal stage as a larva (e.g., benthic polychaete larva) or adult (e.g., jellyfish) to those with very limited dispersal capacity (e.g., a snail with crawl-away larvae). If the dispersive species are more likely to invade estuaries than coasts, but the non-dispersing ones are not, then this hypothesis is supported. Additionally, if species that rely on external fertilization (such as many bivalves) have higher establishment success in estuaries than on the open coast, then the circulation hypothesis is also supported. This type of analysis could readily be carried out on existing datasets of alien species, such as the one included here or that provided by Ruiz et al. (2000), with coding added for dispersal ability. Another approach would be to examine propagule densities of a single alien species with long-distance dispersal. For instance, *Carcinus maenas* larvae spreading on oceanic currents that enter estuaries may be retained and result in higher densities of recruiting juveniles than on the open coast, simply as a function of circulation patterns.

33.4.4 Estuaries Have Undergone More Human Alterations

33.4.4.1 Hypothesis

Estuaries are more invaded than adjacent coastal habitats because their communities offer less biotic resistance as a result of the dramatic anthropogenic alterations they have undergone. Thus native species may be less well adapted to the new conditions than are, by chance, some alien species.

33.4.4.2 General Explanation

Habitats that have been substantially altered by human activities may be particularly vulnerable to invasions by aliens because the environment has been so drastically altered that native species no longer enjoy a home court advantage in context-dependent interactions such as competition (Chap. 14, Byers). Estuaries are arguably the most altered aquatic ecosystems in the world (Edgar et al. 2000). In particular, excessive nutrient inputs have altered biogeochemical cycles, hydrological manipulations (diking, dredging, river diversion, etc.) have changed salinity levels and sedimentation rates, and addition of hard substrates (armored banks, harbor pilings, etc.) has caused a formerly rare habitat type to become quite common (Kennish 2002). Additionally, presence of previously established alien species can be considered an anthropogenically induced alteration, and these may facilitate the establishment and spread of other alien species (Simberloff and Von Holle 1999; Simberloff 2006). In general, open coasts have been far less altered than estuaries. Thus it is plausible that native estuarine invertebrates are less well adapted to current conditions than are their coastal counterparts, and therefore provide less biotic resistance to invasions (Wasson et al. 2005).

33.4.4.3 Support from Global Analysis

A few observations from our dataset support this hypothesis, although without replication the inference is weak. Humans have altered all the estuaries in the study, but those with lowest numbers of aliens (New Hampshire, South Africa) are those that have been less substantially altered, while those with highest numbers of aliens (California, the Netherlands) have been dramatically altered in terms of hydrology, pollution, and addition of hard substrates. In the Netherlands, open coast habitats have also been substantially altered (through hydrological manipulations and addition of hard substrates), and the number of aliens reported from them is higher than in the other seven regions in our study. These observations provide support for this hypothesis, though other explanations must still be invoked to explain why estuaries in the Netherlands are far more invaded than the open coast, since both have been highly altered.

33.4.4.4 Support from Other Observations

Previous studies have suggested that more disturbed marine habitats may be more invaded (e.g., Carlton 1979; Cohen and Carlton 1998; Byers 2002; Kennish 2002), but we do not know of studies with empirical data that compare estuarine and coastal invasions from this perspective.

33.4.4.5 Testable Predications

The most altered estuaries are typically also the ones that have the highest propagule pressure resulting from shipping and other vectors, which confounds testing of this hypothesis. It would be interesting to examine smaller estuaries without major shipping ports, to test the prediction that those with more alterations are more invaded than those with fewer ones. The same comparison could be carried out systematically for open coastal habitats with more vs fewer alterations.

To test the assumptions underlying this explanation, it would be important to determine whether native species indeed provide weaker biotic resistance (e.g., competition or predation) under altered conditions. Experiments to test consumption of resources under polluted vs more pristine conditions, or natural vs altered salinity regimes, would begin to address this question. One such example is Byers (2002) who examined whether alien species performed better under the altered vs natural conditions in the introduced range. He found that under low oxygen conditions (typical of eutrophic conditions) the survival rate of an alien snail (*Batillaria attramentaria*) was significantly higher than that of a native competitor, (*Cerithidea californica*). Such experiments could be complemented by an assessment of physical conditions in the home ranges of successful alien species. One would predict that home conditions would resemble those in the altered invaded range, e.g., a species from naturally nutrient-enriched estuaries should be likely to invade newly eutrophic estuaries elsewhere.

33.4.5 Estuaries Have More "Empty Niches"

33.4.5.1 Hypothesis

Estuaries are more invaded than adjacent coastal habitats because their communities offer less biotic resistance as a result of their lower native species richness related to their recent evolution or harsh conditions.

33.4.5.2 General Explanation

Alien species invading estuaries may face weaker negative biological interactions (competition, predation, disease) with native species than in adjacent open coast habitats, a concept often colloquially couched in terms of estuaries having more "empty niches" than the adjacent open coast (Wolff 1973, 1999; Carlton 1979; Cohen and Carlton 1998). This concept is particularly relevant to upper reaches of estuaries, where there is little representation by native marine species of the open coast, and where distinctive estuarine species – and often not many natives – are found. Conditions in these areas are physiologically challenging, with daily and seasonal fluctuation in salinity and temperature. Species richness is often low in harsh environments (Menge and Sutherland 1976; Nehring 2006), such as the upper reaches of estuaries. Species richness is also a function of habitat size, and estuarine habitats are much more rare than open coast habitats. Low species richness itself is not considered a predictor of low invasion rates at a regional scale – in terrestrial habitats, native and alien species richness are often positively correlated (Levine and D'Antonio 1999; Stohlgren et al. 2003; Chap. 12, Olyarnik et al.). In "mature" or "equilibrium" communities, it appears that the same factors that foster native richness (heterogeneity, moderate environmental conditions, etc.) also support alien species richness (Levine and D'Antonio 1999). However, it has been suggested that estuaries in some regions may not harbor as many species as they could accommodate, perhaps due to recent extinctions or due to insufficient time since their relatively recent geologic formation to allow for speciation or colonization by new species (Jones 1940; Hedgpeth 1968; Wolff 1971; Vermeij 1991). These "empty niches" would thus be available for alien species to fill.

33.4.5.3 Support from Global Analysis

This explanation may be supported by the contrast between invasion rates of the US Pacific and Atlantic coasts. Geologically, Pacific estuaries date back only to end of the last glaciation, while open coast habitats and their associated fauna have been continually present for much longer periods; in contrast, on the Atlantic coast, open coast habitats are geologically younger than most estuaries (Jones 1940; Hedgpeth 1968; Carlton 1979; Cohen and Carlton 1998; Ruiz et al. 2000; Emmett et al. 2000). The geologic youth of Pacific estuaries could explain their high numbers of aliens while the presence of a more ancient estuarine fauna on the Atlantic coast might explain why fewer alien species are established there. According to this hypothesis, one would also expect higher invasion rates on the open coast of the Atlantic than the Pacific. However, the absolute numbers of aliens reported from the coast of New Hampshire vs California are comparable – and very low – though the percentage of the fauna that is alien is markedly higher in New Hampshire (21%) vs California (1.5%).

33.4.5.4 Support from Other Observations

Data from San Francisco Bay suggest that alien species continue to accumulate, at a startling rate of one successful establishment every 14 weeks (Cohen and Carlton 1998); new invasions are apparently successful without displacing natives or earlier established aliens. This suggests that there were "empty niches" to be filled – that biotic interactions such as competition or predation were not intense enough to hamper establishment. This is in contrast to results from terrestrial habitats, where comparably high numbers of established aliens are typical in areas that are native biodiversity "hotspots" (e.g., California grasslands); there is a positive correlation between alien and native diversity at a broad regional scale (Stohlgren et al. 2003). Estuaries thus appear to provide an interesting example where the highest numbers of aliens are found in a habitat with the fewest native species (Wolff 1973, 1999). In contrast, the extremely low invasion rates (<2%; Wasson et al. 2005) of the Pacific coast in the same region as San Francisco Bay occur in one of the most species rich marine habitat types in temperate zones (though this pattern is also likely related to differing propagule pressure; see first hypothesis). Therefore, at least superficially in marine systems, invasion rates may be negatively correlated with native diversity, even if the underlying mechanisms relate more to "empty niches" and relatively depauperate communities than to low species numbers per se. However, along the US Pacific coast, numbers of both alien and native invertebrates decline from south to north (Ruiz et al. 2000; Townsend et al. 2000), refuting a simple inverse relationship between native and alien species numbers, and supporting instead the concept of "empty niches" as predictors of invasions. For terrestrial systems, several studies have examined the scale-dependence of relationships between species richness, diversity, and invasibility (Levine and D'Antonio 1999; Shea and Chesson 2002; Davies et al. 2005). However, for marine systems, examination of the scale-dependence of relationships between species richness, diversity, and invasions appears a fruitful area for further research.

33.4.5.5 Testable Predictions

In order to test the underlying assumption of this hypothesis, one could compare survival or growth of individuals of a broadly tolerant alien species in treatments excluding competitors or predators vs controls, in estuarine vs coastal habitats. If this hypothesis is supported, the alien species' fitness should be much more similar between caged treatment and control in the estuary than on the open coast.

To assess rigorously whether geologic age and evolutionary history indeed affect estuarine vs coastal invasion rates, one could perform more thorough, replicated analyses of the sorts carried out here, comparing numbers and proportions of aliens in regions where estuaries are geologically younger vs older than adjacent open coasts.

33.5 Directions for Future Research

As we prepared this global assessment of estuarine vs coastal invasion rates, it became clear how few consistently collected data are available for robust bioregional comparisons. Of the more than 70 invasion experts we contacted around the world, only 7 were able to provide data on both the target habitat types, and only 4 of those had data for both native and alien species. By far the most frequent response to our query was that data were only available for estuarine habitats, and only for aliens. This highlights the need for investigations that include multiple habitat types, and both native and alien species. An ideal sampling regime would be one that examines the same taxa, with the same methods and substrates (e.g., infaunal polychaetes sampled with benthic cores in low intertidal soft sediments; bryozoans on subtidal settlement plates; decapod crustaceans in traps), across habitat types and regions. Only with this sort of consistency can strong conclusions about habitat and regional differences be drawn. By sampling natives and aliens, invasion rates, not simply counts of aliens, can be analyzed. Finally, consistently sampling both within and outside of harbors in estuaries vs open coasts would allow for testing of hypotheses invoking differential introduction vs establishment success in these areas. Establishment of alien species outside harbors is also of much greater conservation concern than invasion of harbors; hence, focus on non-harbor habitats would be welcome from this perspective. To test among the five hypotheses outlined above, care must be taken to design correlative or manipulative experiments that avoid confounding of different causal factors. In particular, it is critical to separate the effects of differential propagule pressure (the first hypothesis) and habitat-matching (the second hypothesis) from other factors affecting establishment and spread (the remaining three hypotheses).

33.6 Conclusions

The global dataset compiled from eight temperate regions revealed that overall, estuaries harbor more alien invertebrate species than adjacent open coasts, but the magnitude of this difference varies regionally. The majority of the 198 alien species reported from all sites occur in at least some regions in estuaries; only 9 of them occur solely in coastal habitats. Four datasets that documented both native and alien species revealed that the proportion of the invertebrate fauna surveyed that is alien is generally higher in estuaries than on coasts. This trend was pronounced in Central California, weaker in Argentina and the Netherlands, and absent in New Hampshire.

Multiple mechanisms may account for the differences in invasion rates between estuaries and adjacent coasts. Propagule pressure is likely higher in estuaries, and estuarine species that are transported are more likely to establish in estuarine than coastal regions in the recipient regions. Establishment may also be higher in estuaries due to higher retention of dispersive stages and lower levels of negative biotic interaction, due to natives being poorly adapted to anthropogenically altered conditions in estuaries or due to the presence of "empty niches" in relatively depauperate and geologically young estuarine assemblages. Rigorous experimental studies and consistent biogeographic comparisons should be carried out to test these and other hypotheses about habitat differences in marine invasion rates. The answers derived from such studies would inform management practices and control strategies for alien species, which are one of the biggest threats to the integrity of marine and estuarine ecosystems.

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References

Andréfouët S, Zubia M, Payri C (2004) Mapping and biomass estimation of the invasive brown algae *Turbinaria ornate* (Turner) J. Agardh and *Sargassum mangarevense* (Grunow) Setchell on heterogeneous Tahitian coral reefs using 4-meter resolution IKONOS satellite data. Coral Reefs 23(1):26–38

Byers JE (1999) The distribution of an introduced mollusk and its role in the long-term demise of a native confamilial species. Biol Invas 1(4):339–353

Byers JE (2002) Impact of non-indigenous species on natives enhanced by anthropogenic alteration of selection regimes. Oikos 97(3):449–458

Campbell ML, Hewitt CL (1999) Marine biological invasions of Port Phillip Bay, Victoria. CRIMP Technical Report Number 20. CSIRO Marine Research, Hobart, Australia, p 45

Carlton JT (1979) History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. Ph.D. Dissertation, Ecology, University of California, Davis

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

Carlton JT (1989) Man's role in changing the face of the ocean: biological invasions and implications for conservation of near-shore environments. Conserv Biol 3(3):265–273

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

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

Cohen AN, Carlton JT (1995) Nonindigenous aquatic species in a United States estuary: a case study of the biological invasions of the San Francisco bay and delta. A report for the United States Fish and Wildlife Service, Washington D.C. and The National Sea Grant College Program Connecticut Sea Grant (NOAA Grant Number NA36RG0467)

Cohen AN, Carlton JT (1998) Accelerating invasion rate in a highly invaded estuary. Science 279:555–558

Cohen AN, Carlton JT, Fountain MC (1995) Introduction, dispersal and potential impacts of the green crab, *Carcinus maenas* in San Francisco Bay, California. Mar Biol 122:225–237

Davies KF, Chesson P, Harrison S, Inouye BD, Melbourne BA, Rice KJ (2005) Spatial heterogeneity explains the scale dependence of the native-exotic diversity relationship. Ecology 86:1602–1610

Dolgikh AV (1969) Invasion of Hydrobia-ventrosa of the Tiligul estuary by microphallidae larvae. Vestn Zool 3(4):32–35

Edgar GJ, Barrett NS, Graddon DJ, Last PR (2000) The conservation significance of estuaries: a classification of Tasmanian estuaries using ecological, physical and demographic attributes as a case study. Biol Conserv 92:383–397

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

Emmett R, Llansó R, Newton J, Thom R, Hornberger M, Morgan C, Levings C, Copping A, Fishman P (2000) Geographic signatures of North American West coast estuaries. Estuaries 23(6):765–792

Grosholz ED, Ruiz GM (1995) Spread and potential impact of the recently introduced European green crab, *Carcinus maenas*, in central California. Mar Biol 122:239–247

Hedgpeth JW (1968) Newcomers to the Pacific coast: the estuarine itinerants. In: Ricketts EF, Calvin J, Hedgpeth JW (eds) Between Pacific tides, 4th edn. Stanford University Press, Stanford, pp 376–380

Hewitt CL, Campbell ML, Thresher RE, Martin RB (1999) Marine biological invasions of Port Phillip Bay, Victoria. Crimp technical report number 20. December 1999

Jones LL (1940) An introduction of the Atlantic crab into San Francisco Bay. Proceedings of the 6th Pacific Scientific Congress, vol 3, pp 485–486

Kennish MJ (2002) Environmental threats and environmental future of estuaries. Environ Conserv 29(1):78–107

Lee H II, Thompson B, Lowe S (2003) Estuarine and scalar patterns of invasion in the soft-bottom benthic communities of the San Francisco Estuary. Biol Invas 5:85–102

Levine JM, D'Antonio CM (1999) Elton revisited: a review of evidence linking diversity and invasibility. Oikos 87:15–26

Little C (2000) The biology of soft shores and estuaries. Oxford University Press, New York, NY, USA, p 133

Lodge DM (1993) Biological invasions: lessons for ecology. Trend Ecol Evol 8:133–137

Menge BA, Sutherland JP (1976) Species diversity gradients synthesis of the roles of predation competition and temporal heterogeneity. Am Nat 110(973):351–369

Minchin D, Eno C (2002) Exotics of coastal and inland waters of Ireland and Britain. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive aquatic species of Europe: distribution, impact and management. Kluwer, Dordrecht, pp 267–275
Nehring S (2006) Four arguments why so many alien species settle into estuaries, with special reference to the German river Elbe. Helgo Mar Res 60:127–134
Reise K, Gollasch S, Wolff WJ (1999) Introduced marine species of the North Sea coasts. Helgo Meeresunters 52:219–234
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 AN (2000) Invasion of coastal marine communities in North America: apparent patterns, processes, and biases. Annu Rev Ecol Evol Syst 31:481–531
Schwindt E, Francesco CGD, Iribarne OO (2004) Individual and reef growth of the invasive reef-building polychaete *Ficopomatus enigmaticus* in a south-western Atlantic coastal lagoon. J Mar Biol Assoc U K 84(5):987–993
Shea K, Chesson P (2002) Community ecology theory as a framework for biological invasions. Trend Ecol Evol 17:170–176
Simberloff D (2006) Invasional meltdown 6 years later: important phenomenon, unfortunate metaphor, or both? Ecol Lett 9:912–919
Simberloff D, Von Holle B (1999) Positive interactions of nonindigenous species: invasional meltdown? Biol Invas 1:21–32
Steffani CN, Branch GM (2003) Growth rate, condition, and shell shape of *Mytilus galloprovincialis*: responses to wave exposure. Mar Ecol Prog Ser 246:197–209
Stohlgren TJ, Barnett DT, Kartesz JT (2003) The rich get richer: patterns of plant invasions in the United States. Front Ecol Environ 1(1):11–14
Townsend CR, Harper JL, Begon M (2000) Essentials of ecology. Blackwell Science, Malden, MA, USA, pp 552
Tyrrell MC (2002) Impacts of the introduced crab species, *Carcinus maenas* and *Hemigrapsus sanguineus,* in northern New England. Ph.D. Dissertation, University of New Hampshire
Vermeij GJ (1991) When Biotas meet: understanding biotic interchange. Science 253:1099–1104
Wasson K, Zabin CJ, Bedinger L, Diaz MC, Pearse JS (2001) Biological invasions of estuaries without international shipping: the importance of intraregional transport. Biol Conserv 102:143–153
Wasson K, Fenn K, Pearse J (2005) Habitat differences in marine invasions of central California. Biol Invas 7:935–948
Wolff WJ (1971) Origin and history of the brackish-water fauna of NW Europe. Proc 5th European Mar Biol Symposium. Piccin Editore, Padova, pp 11–18
Wolff WJ (1973) The estuary as a habitat. An analysis of data on the soft-bottom macrofauna of the estuarine area of the rivers Rhine, Meuse, and Scheldt. Zool Verh Leiden 126:1–242
Wolff WJ (1999) Exotic invaders of the meso-oligohaline zone of estuaries in the Netherlands: why are there so many? Helgo Meeresunters 52:393–400
Wolff WJ (2005) Non-indigenous marine and estuarine species in the Netherlands. Zool Meded Leiden 79:1–116