Chapter 2
Deep Invasion Ecology and the Assembly of Communities in Historical Time

James T. Carlton

"With dim light and tangled circumstance …"

– George Elliott, *Middlemarch: A Study of Provincial Life (1871)*

2.1 Introduction

A critical component of – and a limitation on – interpreting community structure is a detailed understanding of the ecological and evolutionary history of the assemblage of species in question. There are thus compelling reasons to understand, and seek to measure, how communities have changed over both evolutionary (geological) and ecological (historical) time. Vast waves of change have swept across the Earth in the past one to two millennia as waves of humans invaded across the planet in sequential episodes of exploration, colonization, and urbanization. As an expected and inexorable result of human activity, alterations in biodiversity have impacted terrestrial, freshwater, and marine communities. These alterations include the addition of species (invasions), the deletion of species (extinctions), and altered population dynamics (such as decreasing or increasing the abundance of a species, or altering genetic structure). In even seemingly "pristine" areas – such as wave-exposed high-energy rocky intertidal shores – it is no longer tenable to assume that communities and ecosystems have remained unaltered, in part because of *supply-side impacts* – impacts that are the indirect cascades of human activity originating outside of the area in question (e.g., Butman et al. 1995; Chap. 7, Johnston et al.).

Three (among a number of) reasons drive the interest to understand the first of these alterations – the role of invasions in historical time:

1. An academic desire to understand whether community-level processes, such as predation, competition, and disturbance (Chap. 14, Byers; Chap. 16, Crooks; Chap. 17, Grosholz and Ruiz; Chap. 15, Rilov) derive in part from species interactions on an evolutionary-time scale, or from interactions on an ecological-historical time

scale, such as might be due to the presence of recently-arrived species (Mooney and Cleland, 2001; Grosholz 2002, 2005; Sax et al. 2005; Strauss et al. 2006; Freeman and Byers 2006; Cadotte et al. 2006).

2. A desire that merges academic interests with management concerns to predict what phenomena and processes characterize invaders and invasible habitats (Ricciardi and Rasmussen 1998; Bax et al. 2001; Kolar and Lodge 2001; Chap. 7, Johnston et al.; Chap. 8, Miller and Ruiz; Chap. 10, Smith; Chap. 11, Torchin and Lafferty; Chap. 12, Olyarnik et al.)

3. An interest in establishing the scale of community alteration, in order to undertake environmental management if not actual restoration (Byers et al. 2002; Lotze et al. 2006; Chap. 21, Hacker and Dethier).

The foundation of all three rationales relies not only on the ability to recognize which species are introduced (Chapman and Carlton 1991, 1994) – and thus to make an adequate estimate of the number of non-native species – but also, based on this recognition, to determining experimentally the role of invasions in regulating and producing community structure. However, while many studies that attempt to assess the diversity of invasions acknowledge that the number of invaders is likely underestimated, there has been little attempt to formalize the sources of this underestimation, nor, more importantly, how such partial assessments of the scale of invasions (spatially and temporally) may influence our understanding of the evolution, ecology, history, and management of communities, or of our ability to predict invasions. Clearly, if we have only a partial view of the diversity of non-native species, this compromises our ability to predict what types of organisms can invade, to assess what environments and regions are more or less susceptible to invasions, and to understand invasion patterns over time and space.

The challenges – not mutually exclusive – in estimating the diversity of invaders in a community are shown in Box 2.1. Some of these, as noted below, are universal to any attempt to estimate alpha diversity, but are discussed here specifically as contributors to the underestimation of historical components of community assembly. Discussed here are 12 potential sources of error that have led to invader underestimation, together with some of the implications of such underestimations. The number of introduced species may, of course, also be overestimated, as discussed below as well.

2.2   Invader Underestimation – Systematics

2.2.1   Cryptogenic Species

Species that cannot be reliably demonstrated as being either introduced or native are cryptogenic (Carlton 1996). Most species that are now categorized as cryptogenic were previously treated as native; in turn, many species that should be

recognized as cryptogenic are still regarded as native, the classic categorical default in biogeography and evolutionary biology. Few species previously treated as introduced have been converted to cryptogenic status, in part because the designation of a species as non-native has usually come about as the result of the application of conservative criteria.

Cryptogenic species have been recognized in marine habitats, to some extent in freshwater habitats, and rarely in terrestrial habitats. Cryptogenic species may include unidentified species if there is strong evidence that they may be introduced, but it is important to emphasize that not all unidentified species are cryptogenic (or native). Such evidence is reviewed by Chapman and Carlton (1991, 1994) and includes association with a nonindigenous facies, association with a "weedy" habitat, being a member of a genus or family that is otherwise not known from the region in question (but occurs elsewhere in the world), and other criteria.

Cryptogenic species are not introduced species of uncertain geographic origin, as used by Jensen and Knudsen (2005). No one term captures these "Flying Dutchmen," species that roam the seas on ships with no (as yet) certain home. Cryptogenic species are not introduced species whose mechanism of introduction is uncertain, as used by Englund (2002). The term to be used in this case is polyvectic (Carlton and Ruiz 2005). Cryptogenic species are not solely non-native species or "cryptic invaders," as used by Lockwood et al. (2007). By definition, it is not known if cryptogenic species are native or introduced.

Further, cryptogenic species do not automatically include species with a type locality outside of the region under study, such as the numerous taxa bearing European names on the Pacific coast of North America. In such cases, biogeographic and historical taxonomic considerations come into play. On the one hand, a substantial number of morphotaxa appear to drape naturally along the four northernmost coasts of the Pacific and Atlantic Oceans (northeastern Pacific, northwestern Pacific, northeastern Atlantic, and northwestern Atlantic) as a result of their Tertiary histories of evolution, expansion and contraction, but whether these remain the same genospecies (a taxon characterized by identical genomes throughout its range) is not known for most of these taxa. Transarctic species embrace a wide phyletic range: examples include the eelgrass *Zostera marina*, the sea anemone *Metridium senile*, the seaslugs *Alderia modesta* and *Dendronotus frondosus*, the barnacles *Balanus balanus* and *Semibalanus balanoides,* the priapulid *Priapulus caudatus*, and the mussels *Mytilus trossulus* and *Modiolus modiolus*. Coan et al. (2000) list more than 40 species of bivalve mollusks that are considered circumboreal.

On the other hand, nineteenth and early twentieth century monographs of European taxa ranging from foraminiferans to polychaetes to algae were used for many decades to identify species from around the world: the taxonomic residue of this globalization of euronomenclature remains with us in the form of perhaps thousands of undescribed (not introduced!) species bearing European names in

Africa, South America, North America, Asia, and Australasia. A rocky shore sea-weed in California with a type locality of Italy would thus bear reexamination. Much of this early work served to lead to the misconception that many shallow-water marine organisms were "cosmopolitan". While many "cosmopolitan" species may in theory be considered cryptogenic, as their modern-day global distribution could be the result of centuries of international shipping, it is argued below that a more conservative (although vexing) approach is to consider many of these taxa to be undetermined – essentially now unidentified or unidentifiable species, pending systematic revisions.

2.2.2   Pseudoindigenous Species

An important but largely overlooked source of underestimating invasion diversity in a given region is the presence of *pseudoindigenes*, here defined as introduced species that are mistakenly considered as native (indigenous or endemic) to a location. Pseudoindigenes include four categories of taxa (Box 2.1). The level of sophistication of systematic and biogeographic knowledge predicts that there are more examples of category 1 than category 2, and more examples of category 2 than category 3, as explained below. Category 4 is conceptually distinct from the first three, and does not fall into this pattern.

Category 1: introduced species re-described as new after introduction, although already described in their native region Pseudoindigenes in this first category are common. Table 2.1 presents 94 introduced species redescribed as "new", following their introduction to a region. In many cases these species have

---

Box 2.1 Sources of error in estimating the number and thus importance of introduced species

SYSTEMATICS

Cryptogenic Species (*cryptogens***)**

Species that cannot be reliably demonstrated as being either introduced or native.

Pseudoindigenous Species (*pseudoindigenes***)**

Introduced species mistaken as native (indigenous or endemic) species:

1. Species redescribed as new after introduction, although already described in their native region (Table 2.1).
2. Species first described as new after introduction, and later found elsewhere (Table 2.2).

Box 2.1 (continued)

3. Species described as new after introduction, and remaining unknown else-where (Table 2.3).
4. Species misidentified as previously known native species:
   A. Imperfect taxonomy
   B. Cryptic genospecies invasions

Unidentified Species, including many "**Cosmopolitan**" **Species**
Species that are not (unidentified) or cannot yet be (unidentifiable) identified to a level permitting biogeographic assessment.
Small Species
Species typically less than 1 mm in size that – *because of their size* – are con-sidered naturally distributed ("smalls rule").
Uninvestigated Taxa
Species groups that are not or rarely studied.
Known but Unreported Taxa
Introduced species known to researchers but never published.
BIOGEOGRAPHY and COMMUNITY HISTORY
Widespread Intraoceanic Species
Species with *within*-ocean distributions that appear to mirror presumptive natural patterns.
Widespread Interoceanic Corridor Species
Species with *between*-ocean distributions that appear to mirror presumptive natural patterns.
Neritic Species with Presumptive Oceanic Dispersal
Species with planktonic life-history stages or living on floating habitats that are presumed to be amenable to dispersal on oceanic currents.
Resident Species
Introduced or cryptogenic species which, after a length of time, are grouped with the "native" component.
SAMPLING
Species in Underexplored Habitats and Associations

1. Undersampled parasitic, commensal, or symbiotic introduced species.
2. Undersampled introduced species in microhabitats and ecotonal habitats.

Incipient Invasions: Species with Small Population Sizes
Newly established introductions with small, restricted populations.

been described as new in several regions (up to 11 times for a single species), each time with a different name, to a total of 159 cases of mistaken re-descriptions. No systematic or focused search for pseudoindigenes in this category has been under-taken in any biota, and thus neither the regional nor global scale of this underesti-mation of introductions (and overdescription of biodiversity) is known. A few

Table 2.1 Examples of introduced species mistakenly redescribed as native species after their introduction or appearance in a new region

Species	Native to	Redescribed as (from)	Reference
Ciliophora (ciliates)			
Ancistrocoma pelseneeri Chatton & Lwoff, 1926	North Atlantic	Parachaenia myae Kofoid & Bush, 1936 (California)	Kozloff (1946)
Hydrozoa (hydroids)			
Obelia bidentata Clark, 1875	North Atlantic	Obelia corona Torrey, 1904 (California)	Cornelius (1975)
		Obelia multidentata Fraser, 1914 (Washington)	Cornelius (1975)
Cladonema radiatum Dujardin, 1843	North Atlantic	Cladonema novae-zelandiae Ralph, 1953 (New Zealand)	Schuchert (1996)
Pinauay crocea (Agassiz, 1862)	North Atlantic	Parypha microcephala Agassiz, 1865 (California)	Torrey (1902)
		Tubularia elegans Clark, 1876 (California)	Torrey (1902)
Cordylophora caspia (Pallas, 1771)	Ponto-Caspian	Cordylophora lacustris Allman, 1844 (Ireland)	Schuchert (2004)
		Cordylophora albicola Kirchenpauer, 1861 (Germany)	Schuchert (2004)
		Cordylophora americana Leidy, 1870 (Atlantic American coast)	Schuchert (2004)
		Cordylophora whitelegii von Lendenfeld, 1887 (Australia)	Briggs (1931)
		Cordylophora fluviatilis Hamilton, 1928 (New Zealand)	Briggs (1931)
		Cordylophora lacustris otagoensis Fyfe, 1929 (New Zealand)	Schuchert (2004)
Pennaria disticha Goldfuss, 1820	North Atlantic	Corydendrium splendidum Boone, 1938 (Hawaii)	Cooke (1977)
Garveia franciscana (Torrey, 1902)	South Pacific-Indian Ocean	Bimeria monodi Billard,1927 (Cameroon)	Vervoort (1964) (all Garveia franciscana)
		Bimeria tunicata Fraser, 1944 (Louisiana)	
		Perigonimus megas Kinne, 1956 (Netherlands)	
Gonionemus vertens Agassiz, 1862	North Pacific	Haleremita cumulans Schaudinn, 1894 (Germany: Berlin Aquarium)	Edwards (1976)
		Gonionemus murbachi Mayer, 1901 (Massachusetts)	Kramp (1961)

	Gonionemus vindobonensis Joseph, 1918 (Adriatic: Trieste, in an aquarium)	Kramp (1961)
Northwest Atlantic	*Nemopsis heteronema* Haeckel, 1879 (Norway)	Kramp (1961)
	Nemopsis crucifera (Forbes & Goodsir, 1853) (Scotland)	Kramp (1961)
Craspedacusta sowerbii Lankester, 1880 China	*Microhydra ryderi* Potts, 1885 (Pennsylvania)	Kramp (1961)
	Microhydra germanica Roch, 1924 (Germany)	Kramp (1961)
Anthozoa (sea anemones)		
Diadumene lineata (Verrill, 1873)	Japan	*Sagartia luciae* Verrill, 1898 (Connecticut)	Manuel (1988)
Turbellaria (flatworms)		
Rhynchodemus bilineatus (Mecznikov, 1866)	Europe	*Rhynchodemus sylvaticus* (Leidy, 1851) (Philadelphia, Pennsylvania)	Ogren (1989a)
	Rhynchodemus americanus Hyman, 1943 (Missouri)	Ogren (1989a)
Bipalium kewense Moseley, 1878	Indo-Pacific, Japan	*Bipalium manubriatum* Sharp, 1891 (Pennsylvania)	Ogren (1984)
	Bipalium costaricense Hyman, 1939 (Costa Rica)	Ogren (1984)
Polychaeta (worms)		
Myrianida pachycera (Augener, 1913)	Indo-West Pacific	*Myrianida crassicirrata* Hartmann-Schröder, 1965 (Oahu, Hawaiian Islands)	Nygren (2004)
Polydora cornuta Bosc, 1802	Northwest Atlantic	*Polydora amarincola* Hartman, 1936 (California)	Blake and Maciolek (1987)
Streblospio benedicti Webster, 1879	Northwest Atlantic	*Streblospio lutincola* Hartman, 1936 (California)	Carlton (1979)
Pseudopolydora kempi (Southern, 1921)	Japan	*Neopygopsio laminifera* Berkeley & Berkeley, 1954 (British Columbia)	Banse (1972)
Neanthes succinea (Frey & Leuckart, 1847)	Northwest Atlantic	*Nereis saltoni* Hartman, 1936 (California)	Carlton (1979)
Janua pagenstecheri (Quatrefages, 1865) Europe	*Spirorbis unicornis* Bailey & Harris, 1968 (Galapagos Islands)	Knight-Jones et al. (1975)
	Spirorbis epichysis Bailey, 1970 (West Indies)	Knight-Jones et al. (1975)
Simplicaria pseudomilitaris (Thiriot-Quievreux, 1965)	Atlantic Ocean	*Spirorbis regalis* Bailey & Harris, 1968 (Galapagos Islands)	Vine et al. (1972)

(continued)

Table 2.1 (continued)

Species	Native to	Redescribed as (from)	Reference
Hydroides elegans (Haswell, 1883)	Australasia	*Hydroides pectinata* Lo Bianco, 1893 (Italy)	Zibrowius (1971)
		Hydroides trypanon Saint-Joseph, 1906 (Italy)	
		Hydroides pacificus Hartman, 1969 (California)	
Gastropoda (snails)			
Crepidula plana Say, 1822	Northwest Atlantic	*Crepidula sinuosa* Turton, 1825 (boat hull, Yorkshire, England)	Collin (2000)
Potamopyrgus antipodarum (Gray, 1843)	New Zealand	*Hydrobia jenkinsi* Smith, 1889 (England)	Ponder (1988)
Truncatella pulchella Pfeiffer, 1839	Northwest Atlantic	*Truncatella bairdiana* C. B. Adams, 1852 (Pacific Panama)	Clench and Turner (1948)
Corambe obscura (Verrill, 1870)	Northwest Atlantic	*Corambe batava* Kerbert, 1886 (Netherlands)	Swennen and Dekker (1995)
		Corambella carambola Marcus, 1955 (Brazil)	
Haminoea japonica (Pilsbry, 1895)	Japan	*Haminoea callidegenita* Gibson & Chia, 1989 (Washington)	Gosliner and Behrens (2006)
Siphonaria pectinata (Linnaeus, 1758)	Eastern Atlantic	*Siphonaria lineolata* d'Orbigny, 1841 (Cuba)	Carlton (1992)
		Siphonaria naufragum Stearns, 1872 (Florida)	Rosenberg (2005)
Ferrissia fragilis (Tryon, 1863)	North America	*Ferrissia wautieri* Mirolli, 1960 (Europe)	Walther et al. (2006)
Myosotella myosotis (Draparnaud, 1801)	Europe	*Melampus borealis* Conrad, 1832 (Rhode Island)	Martins (1996) (all *M. myosotis*)
		Auricula reflexilabris Orbigny, 1837 (Peru)	
		Alexia bermudensis H. & A. Adams, 1855 (Bermuda)	
		Auricula meridionalis Brazier, 1877 (Australia)	
		Auricularia meridionalis Brazier, 1877 (Australia)	
		Alexia acuminata Morelet, 1889 (South Africa)	
		Alexia pulchella Morelet, 1889 (South Africa)	

Species	Native region	Reported as	Reference
		Alexia myosotis marylandica Pilsbry, 1900 (Maryland)	Cowie (1997)
		Alexia subflava Fenaux, 1939 (Bermuda)	Cowie (1997)
Tarebia granifera (Lamarck, 1816)	Indo-Pacific	*Melania mauiensis* Lea, 1856 (Hawaii)	Cowie (1997)
Milax gagates (Draparnaud, 1801)	Europe	*Amalia babori* Collinge, 1897 (Hawaii)	Cowie (1997)
Meghimatium striatum Hasselt, 1824	Asia	*Philomycus australis* Bergh, 1870 (Hawaii)	Cowie (1997)
Allopeas gracile (Hutton, 1834)	Neotropics	*Bulimus junceus* Gould, 1846 (Hawaii)	Cowie (1997)
Paropeas achatinaceum (Pfeiffer, 1846)	Indo-Pacific	*Opeas henshawi* Sykes, 1904 (Hawaii)	Cowie (1997)
Laevicaulis alte (Ferussac, 1822)	Central Africa	*Vaginula leydigi* Simroth, 1889 (Australia)	Cowie (1997)
Hawaiia minuscula (Binney, 1841)	North America	*Helix kawaiensis* Reeve,1854 (Hawaii)	Cowie (1997)
Bivalvia (bivalves)			
Xenostrobus securis (Lamarck, 1819)	Australia/New Zealand	*Limnoperna fortunei kikuchii* Habe, 1981 (Japan)	Kimura et al. (1999)
Mytilus galloprovincialis Lamarck, 1819	Mediterranean	*Mytilus edulis diegensis* Coe, 1945 (California)	Coan et al. (2000)
Mytilopsis sallei (Recluz, 1849)	Eastern Pacific	*Mytilopsis allyneana* Hertlein & Hanna, 1949 (Fiji)	Morton (1981)
Mytilopsis leucophaeata Conrad, 1831	Northwest Atlantic	*Congeria cochleata* (Kickx, 1835) (Belgium)	Marelli and Gray (1983)
		Mytilopsis zeteki Hertlein & Hanna, 1949 (Panama Canal)	Rosenberg (2005)
Crassinella lunulata (Conrad, 1834)	Northwest Atlantic	*Crassinella oregonensis* Keen, 1938 (Oregon)	Coan (1979)
Mya arenaria Linnaeus, 1758	Northwest Atlantic	*Mya hemphilli* Newcomb, 1874 (California)	Carlton (1979)
Chama fibula Reeve, 1846	Philippines	*Chama hendersoni* Dall, Bartsch, & Rehder, 1938 (Hawaii)	Kay (1979)
Mercenaria campechiensis (Gmelin, 1791)	Northwest Atlantic	*Venus apodema* Dall, 1902 (Pacific Panama)	Keen (1971)
Venerupis philippinarum (A. Adams & Reeve, 1850)	Japan	*Mercenaria kennicottii* Dall, 1871 (Washington; probably adventitious shell [Carlton, 1979]).	Coan et al. (2000)
		Paphia bifurcata Quayle, 1938 (British Columbia)	Coan et al. (2000)
Hiatella arctica (Linnaeus, 1767)	Atlantic Ocean	*Saxicava hawaiensis* Dall, Bartsch, & Rehder, 1938 (Hawaii)	Kay (1979)
Martesia striata (Linnaeus, 1758)	South Pacific?	*Martesia hawaiensis* Dall, Bartsch, & Rehder, 1938 (Hawaii)	Kay (1979)

Table 2.1 (continued)

Species	Native to	Redescribed as (from)	Reference
Lyrodus pedicellatus (Quatrefages, 1849)	South Pacific?	*Teredo chlorotica* Gould, 1870 (Masssachusetts, from ships from Pacific Ocean)	Turner (1966) (all *L. pedicellatus*)
		Teredo diegensis Bartsch, 1916 (California)	
		Teredo townsendi Bartsch, 1922 (California)	
		Teredo yatsui Moll, 1929 (Japan)	
		Teredo robsoni Roch, 1931 (South Africa)	
		Teredo tateyamensis Kuronuma, 1931 (Japan)	
		Teredo hawaiensis Dall, Bartsch & Rehder 1938 (Hawaii)	
		Teredo kauaiensis Dall, Bartsch & Rehder,1938 (Hawaii)	
		Teredo taiwanensis Taki & Habe, 1945 (Taiwan)	
		Teredo midwayensis Edmondson, 1946 (Midway Island)	
		Teredo honoluluensis Edmondson, 1946 (Hawaii)	
Psiloteredo megotara Hanley, 1848	Europe	*Teredo dilatata* Sowerby, 1851 (Massachusetts)	Turner (1966)
Bankia bipalmulata (Lamarck, 1801)	South Pacific ?	*Bankia hawaiiensis* Edmondson, 1942; *Bankia konaensis* Edmondson, 1942 (both, Hawaii)	Turner (1966)
Teredo navalis Linnaeus, 1758	South Pacific ?	*Teredo japonica* Clessin, 1893 (Japan); *Teredo beachi* Bartsch, 1921 (California)	Turner (1966) (all *Teredo navalis*)
Teredo bartschi Clapp, 1923	South Pacific ?	*Teredo batilliformis* Clapp, 1924 (Bermuda); *Teredo aegyptia* Roch, 1935 (Suez Canal); *Teredo hiloensis* Edmondson, 1942 (Hawaii)	Turner (1966) (all *Teredo bartschi*)
Teredo clappi Bartsch, 1923	South Pacific ?	*Teredo trulliformis* Miller, 1924 (Hawaii)	Turner (1966)

Teredo furcifera von Marttens, 1894	South Pacific ?	*Teredo parksi* Bartsch, 1921 (Hawaii)	Turner (1966)
Copepoda (copepods)			
Mytilicola orientalis Mori, 1935	Japan	*Mytilicola ostreae* Wilson, 1938 (Washington)	Odlaug (1946)
Ostracoda (ostracodes)			
Eusarsiella zostericola Cushman, 1906	Northwest Atlantic	*Sarsiella tricostata* Jones, 1958 (California)	Kornicke (1967)
Spinileberis quadriaculeata (Brady, 1880)	Japan	*Spinileberis hyalinus* Watling, 1970 (California)	Watling (1975)
Cirripedia (barnacles)			
Balanus amphitrite Darwin, 1854	Indo-Pacific	*Balanus amphitrite hawaiiensis* Broch, 1927 (Hawaii)	Henry and McLaughlin (1975) (all *B. amphitrite*)
		Balanus amphitrite franciscanus Rogers, 1949	
		Balanus amphitrite herzi Rogers, 1949 (both, California)	
Elminius modestus Darwin, 1854	New Zealand	*Elminius cristallinus* Gruvel, 1907 (Azores)	Newman and Ross (1976)
Pollicipes polymerus Sowerby, 1833	Northeast Pacific	*Pollicipes polymerus madrasensis* Daniel, 1953 (India)	Newman and Killingley (1985)
Isopoda (isopods)			
Sphaeroma quoinaum Milne-Edwards,1840	New Zealand	*Sphaeroma pentodon* Richardson, 1904 (California)	Rotramel (1972)
Sphaeroma terebrans Bate, 1866	Indian Ocean	*Sphaeroma destructor* Richardson, 1897 (Florida)	Calman (1921)
Synidotea laevidorsalis (Miers, 1881)	Japan	*Synidotea laticauda* Benedict, 1897 (California)	Chapman and Carlton (1991)
		Synidotea marplatensis Giambiagi, 1922 (Argentina)	Chapman Carlton (1991)
Littorophiloscia culebrae (Moore, 1901)	North Atlantic	*Philoscia dartevellei* Brian, 1953 (Angola)	Taiti and Ferrara (1986)
Niambia capensis (Dollfus, 1895)	Southern Africa	*Porcellio littorina* Miller, 1936 (California)	Jass and Klausmeier (2000)
Porcellio dilatatus Brandt, 1833	Europe	*Porcellio spinicornis occidentalis* Miller, 1936 (California)	Van Name (1940)

(continued)

Table 2.1 (continued)

Species	Native to	Redescribed as (from)	Reference
Porcellio laevis Latreille, 1804	Europe	*Porcellio aztecus* Saussure, 1857 (Mexico)	Van Name (1936) (all *P. laevis*)
		Porcellio cubensis Saussure, 1857 (Cuba)	
		Porcellio mexicanus Saussure, 1857 (Mexico)	
		Porcellio interruptus Heller, 1861 (Chile)	
		Porcellio formosus Stuxberg, 1875 (California)	
		Porcellio parvicornis Richardson, 1902 (Bermuda)	
Porcellio scaber Latreille, 1804	Europe	*Porcellio nigra* Say, 1818 (Eastern United States)	Van Name (1936) (all *P. scaber*)
		Porcellio gemmulatus Dana, 1853 (United States)	
		Philoscia tuberculata Stimpson, 1856 (California)	
		Porcellio montezumae Saussure, 1857 (Mexico)	
Armadillidium vulgare (Latreille, 1804)	Europe	*Armadillo pilularis* Say, 1818 (United States)	Van Name (1936) (all *A. vulgare*)
		Armadillidium pilulare Stuxberg, 1875 (North America)	
		Uropodias bermudensis Richardson, 1902 (Bermuda)	
Amphipoda (amphipods)			
Caprella mutica Schurin, 1935	Japan	*Caprella macho* Platvoet, de Bruyne, & Meyling, 1995 (Netherlands)	Marellli (1981)
Caprella penantis Leach, 1814	North Atlantic?	*Caprella acutifrons neglecta* Mayer, 1890 (Hong Kong, off ship's bottom)	Stoddart and Lowry (2003)
Monocorophium insidiosum (Crawford 1937)	North Atlantic	*Corophium oaklandense* Shoemaker, 1949 (California)	Chapman (2007)

Stomatopoda (mantis shrimp)			
Gonodactylaceus falcatus (Forskal, 1775)	Indo-Pacific	*Gonodactylus aloha* Manning & Reaka, 1981 (Hawaii)	Ahyong (2001)
Decapoda (crabs)			
Rhithropanopeus harrisii (Gould, 1841)	Northwest Atlantic	*Pilumnus tridentatus* Maitland, 1874 (Netherlands)	Buitendijk and Holthuis (1949)
Carcinus maenas Linnaeus, 1758	Europe	*Carcinus granulatus* Say, 1817 (Long Island Sound)	Carlton and Cohen (2003)
Diptera (flies)			
Telmatogeton japonicus Tokunaga, 1933	Japan	*Telmatogeton remanei* Remmert, 1963 (Baltic Sea)	Kronberg (1986)
Heteroptera (water bugs)			
Trichocorixa reticulata (Guerin-Meneville, 1857)	North America	*Corixa blackburni* White, 1877 (Hawaii)	Zimmerman (1948)
Pycnogonida (sea spiders)			
Pigrogromitus timsanus Calman, 1927	southern hemisphere?	*Clotenopsa prima* Hilton, 1942 (Hawaii)	Stock (1968)
Kamptozoa (entoprocts)			
Urnatella gracilis Leidy, 1851	North America	*Urnatella indica* Seshaiya, 1946 (India)	Enschermann (1987)
Tunicata (sea squirts)			
Botryllus schlosseri (Pallas, 1766)	Europe?	*Botryllus gouldii* Verrill, 1871 (New York)	Van Name (1945)
Styela clava Herdman, 1881	Northwestern Pacific	*Styela mammiculata* Carlisle, 1954 (England)	Millar (1970)
Styela canopus (Savigny, 1816)	Northwestern Pacific	*Cynthia partita* (Stimpson, 1852) (Massachusetts)	Kott (1998) (all *S. canopus*)
		Styela variabilis Hancock, 1868 (England)	
		Cynthia stellifera Verrill, 1871 (Connecticut)	
		Styela canopoides Heller, 1877 (Adriatic Sea)	
		Styela partita bermudensis Van Name, 1902 (Bermuda)	

Table 2.1 (continued)

Species	Native to	Redescribed as (from)	Reference
Styela plicata (Lesueur, 1823)	Northwestern Pacific	*Styela gyrosa* Heller, 1877 (Adriatic Sea)	Kott (1998)
		Styela pinguis Herdman, 1898 (Australia)	Kott (1998)
		Styela barnharti Ritter & Forsyth, 1917 (California)	Abbott and Johnson (1972)
Ascidiella aspersa (Muller, 1776)	Europe	*Ascidiella senegalensis* Michaelsen, 1915 (Senegal)	Monniot et al. (2001)
Ascidiella sydneiensis Stimpson, 1855	Australasia	*Phallusia longitubis* Traustedt, 1882 (West Indies)	Kott (1998)
Ascidia archaia Sluiter, 1890	Indo-West Pacific	*Ascidia corelloides* (Van Name, 1924) (Curacao)	Kott (1985); status as introduced to Caribbean herein
Ciona intestinalis (Linnaeus, 1767)	North Atlantic	*Ascidia diaphanaea* Quoy & Gaimard, 1834 (Australia)	Kott (1998)
		Ciona robusta Hoshino & Tokioka, 1967 (Japan)	Kott (1998)
Osteichthyes (fish)			
Omobranchus punctatus (Valenciennes, 1836)	Indo-Pacific	*Poroalticus sewalli* Foster, 1931 (Trinidad)	Springer and Gomon (1975)
Omobranchus ferox (Herre, 1927)	Philippines	*Omobranchus dealmeida* Smith, 1949 (Mozambique)	Springer and Gomon (1975)
Micropterus salmoides (Lacepède, 1802)	North America	*Pikea sericea* Fowler, 1938 (Hong Kong)	Robins and Böhlke (1960)
Hexanematichthys couma (Valenciennes 1840)	South America	*Sciadeichthys walrechti* Boeseman, 1954 (specimens washed ashore in Netherlands)	Marceniuk and Ferraris (2003)
Rhodophyta (red algae)			
Porphyra suborbiculata Kjellman, 1897	North Pacific	*Porphyra carolinensis* Coll & Cox, 1977 (Western Atlantic)	Broom et al. (2002)
Neosiphonia harveyi (Bailey, 1848)	Asia	*Polysiphonia havanensis insidiosa* J. Agardh, 1863 (Cuba)	Guiry (2003)
		Polysiphonia argentinica W. R. Taylor, 1939 (Argentina)	Guiry (2003)
Spermatophyta (seed plants)			
Zostera japonica (Ascherson & Graebner, 1907)	Western Pacific	*Zostera americana* den Hartog, 1970 (State of Wasington)	Bigley and Barreca (1982)

examples might suffice, but this longer list (although itself doubtless a small fraction of the total phenomenon) serves to illustrate the historical, taxonomic, and biogeographic breadth – the sheer ubiquity – of this category. Included are examples from aquatic (freshwater), marine, and terrestrial habitats.

With the onset of increased systematic work in the early nineteenth century, non-native species began to be mistakenly redescribed as natives (Table 2.1): the European green shore crab *Carcinus maenas* is described as a new species (*Carcinus granulatus*) in 1817 in North America, and, reciprocally, the American slipper limpet *Crepidula plana* is described as a new species (*Crepidula sinuosa*) in 1825 in Europe. The American dreissenid mussel *Mytilopsis leucophaeata* is also described as a new species (*Congeria cochleata*) in 1835 in Europe. As early as the 1830s, European species were being redescribed as native species in the Pacific Ocean, including the seasquirt *Ciona intestinalis* in Australia and the marsh snail *Myosotella myosotis* in Peru, ship-associated animals whose arrival in the Pacific Ocean could date back to the sixteenth century. Species commonly associated with global commerce are redescribed continuously: the Ponto-Caspian hydroid *Cordylophora lacustris* and the European synanthropic isopod *Porcellio laevis* are redescribed at least 6 times each, the European snail *Myosotella myosotis* is carried to South America, North America, Africa, and Bermuda, and redescribed as a new species 9 times, and the shipworm *Lyrodus pedicellatus*, not surprisingly, is redescribed at least 11 times from around the world.

Introductions continue to be redescribed as new taxa (Table 2.2): the Indo-Pacific mantis shrimp *Gonodactylaceus falcatus* was redescribed as a new species in 1981 from the Hawaiian Islands; the Australasian mussel *Xenostrobus securis* was redescribed as new, also in 1981, from Japan; the Indian Ocean seasquirt *Eusynstyela hartmeyeri* was redescribed as a new species from New Caledonia in 1991, and the Japanese skeleton shrimp (caprellid) *Caprella mutica* was redescribed as a new species from Europe in 1995. Kott (2004) described an abundant non-native ascidian (not seen or collected prior to the 1970s) in the New England fauna as an endemic species (*Didemnum vestum*), whose origin remains uncertain (indeed, it may fall into the second category of pseudoindigenes, below). All of these are examples only, and an unknown number of "new" species described from shallow coastal waters, especially harbors and estuaries subjected to the vectors that transport species around the world, are actually redescriptions of species already described from elsewhere in the world.

The lag time in recognizing that an introduced species has been mistakenly redescribed ranges from months to over 100 years. For example, the Japanese clam *Venerupis philippinarum* was mistakenly redescribed from British Columbia in 1938, and the Japanese ascidian *Styela clava* was mistakenly redescribed from England in 1954: in both cases, the error was recognized immediately. On the other hand, it took 125 years to show that a European seaslug, *Corambe batava* (long regarded as an endangered if not extinct species in Europe), was the common American seaslug *Corambe obscura*. Thus a great many pseudoindigenes remain

Table 2.2 Examples of introduced species first described from non-native regions (and later found elsewhere)

Species	Native to	First Described from	Reference
Turbellaria (flatworms)			
Taenioplana teredini Hyman, 1944	Southern hemisphere?	Hawaii	Prudhoe (1985)
Hydrozoa (hydroids)			
Blackfordia virginica Mayer, 1910	Ponto-Caspian	Virginia	Mills and Sommer (1995)
Garveia franciscana (Torrey, 1902)	South Pacific–Indian Ocean	San Francisco Bay	Vervoort (1964)
Pachycordyle navis (Millard, 1959)	Europe?	South Africa (from hull of resident ship)	Schuchert (2004)
Anthozoa (sea anemones)			
Nematostella vectensis Stephenson, 1935	North America	England	Pearson et al. (2002); Darling et al. (2004)
Carijoa riisei (Duchassaing & Michelotti, 1860)	Indo-West Pacific	Caribbean	Kahng (2005)
Clitella (oligochaete worms)			
Branchiura sowerbyi Beddard, 1892	Asia	Regent's Park, London	Cohen and Carlton (1995)
Limnodriloides monothecus Cook, 1974	Western Atlantic	Baja California	Cohen and Carlton (1995)
Gastropoda (snails)			
Babakina festiva (Roller, 1972)	Asia	California	Carlton (1979)
Bivalvia (bivalves)			
Mya arenaria Linnaeus, 1758	North America	North Sea	Coan et al. (2000)
Crassostrea angulata (Lamarck, 1819)	Asia	Europe	Ó Foighil et al. (1998)
Teredicola typica Wilson, 1942	Southern hemisphere?	Hawaii	McKoy (1975)

Isopoda (isopods)			
Iais californica (Richardson, 1904)	New Zealand	California	Rotramel (1972)
Limnoria tripunctata Menzies, 1951	Southern hemisphere	California	Cookson (1991)
Alloniscus oahuensis Budde-Lund, 1885	Indo-Pacific	Hawaii	Taiti and Howarth (1995)
Amphipoda (amphipods)			
Gammarus tigrinus Sexton, 1939	Atlantic North America	England	Bousfield (1973)
Diptera (flies)			
Canaceoides angulatus Wirth, 1969	Tropical Eastern	Hawaii	Englund et al. (2000)
Procanace williamsi Wirth, 1951	Asia	Hawaii	Englund et al. (2000)
Bryozoa (bryozoans)			
Victorella pavida Kent, 1870	Indian Ocean	England	Carlton (1979)
Rhodophyta (red algae)			
Neosiphonia harveyi (Bailey, 1848)	Asia	Connecticut	McIvor et al. (2001)
Spermatophyta (higher plants)			
Spartina alterniflora (Loisell, 1815)	North America	Bayonne, France	Mobberley (1956)

unrecognized, particularly in the face of declining taxonomic expertise required to ferret out such taxa.

The common early failure to recognize invasions as introductions can be understood in the context of the challenges of having access to sufficient literature, combined with an underappreciation for the potential of non-native species to appear at a systematist's doorstep. The failure to continue to do so in the twentieth and twenty-first centuries lies at several doorsteps, including the spread of species that are members of complexes difficult to tease apart morphologically, concomitant with increasing globalization and speed of commerce, leading to the requirement to be a master of the world's biota, a challenge for even specialized systematists. The lack of global knowledge of specific groups explains in large part the failure of many "environmental impact surveys" to report new invasions, as those workers involved in making routine identifications of marine invertebrates often do not possess global-scale expertise.

Whether newer or older invasions, the presence of anomalous clades in a biota does not always attract the attention of systematists. The "Californian" isopod *Sphaeroma pentodon* took many years to be accepted by North American workers as the Australian-New Zealand isopod *Sphaeroma quoianum*, despite the fact that the speciose genus *Sphaeroma* is centered in the western Pacific and Indo-Pacific, and no other species of *Sphaeroma* other than *S. pentodon* was known from the Northwest Pacific Ocean north of 25° north latitude. Monogeneric species occurring in oceans thousands of kilometers away from their closest evolutionary relatives or away from where the genus is otherwise represented by many species would bear reexamination relative to their biogeographic affinities and history, and thus perhaps their true identity.

Category 2: introduced species first described as new after introduction, and later found elsewhere As a result of species being transported from a region where the biota is poorly described to a region under greater biological and systematic scrutiny, a number of invasions have been first described in areas where they are not native. Twenty-one examples of such species that were then later discovered in their native, or other regions, are shown in Table 2.2. Fewer examples of these are available than those in the previous category, because the necessary "matches" require sophisticated global knowledge and, of course, sufficient exploration in native regions. Thus, the type locality of a species does not necessarily imply where a species is native. For the Hawaiian Islands, Cowie (1998) has noted that "It was only in the middle of the nineteenth century that naturalists really began to take note of the Hawaiian biota, describing many new, supposedly endemic species … Six of the ten introduced species first recorded between 1840 and 1889 were originally described from the Hawaiian Islands."

There may be equally long lag times in resolving where such species are native (introduced species that were described from a non-native region but that have not yet been found elsewhere are discussed in the next category). The common and widespread Atlantic North American filamentous red alga, *Neosiphonia harveyi* (= *Polysiphonia harveyi*), described in 1848 from Connecticut, was not recognized as

native to Asia until the 1990s (McIvor et al. 2001). This species is further discussed below in two contexts, relative to biogeographic biases in detecting invasions, and relative to the concept of the "Missing 1000" invasions (Carlton 2000, 2002, and below).

One of the more famous invasions in this category (or perhaps the first, above) is the case of the appearance of an Asian oyster in the genus *Crassostrea* in the European theater about 500 years ago. Described by Lamarck in 1819 as a native southern European species, *Ostrea angulata* (now *Crassostrea angulata*), and long known as the "Portuguese oyster," investigators had concluded by the 1940s that it was identical with the Japanese *C. gigas*. However, recent work suggests that *C. angulata* may be a genetically distinct (although morphologically identical) sibling species of *C. gigas* (Ó Foighil et al. 1995, 1998; Boudry et al. 1998; Huvet et al. 2000, 2004; Lapegue et al. 2004; P. Gaffney, personal communication). If the two are not the same, *C. angulata* represents a case similar to that of *Mya arenaria* and *Spartina alterniflora*, noted below, although the recognition of *C. angulata* as a distinct genospecies in Asia has taken nearly 300 years.

Of interest is that two iconic marine organisms native to the American Atlantic coast were first described from Europe: the edible soft-shell clam *Mya arenaria* was described from the North Sea by Linnaeus in 1758 (what could not be known to Linnaeus was that it was introduced centuries earlier by the Vikings from North America), while the salt marsh cordgrass *Spartina alterniflora* was first described from France in 1815 (to where it had been introduced, perhaps by shipping, presumably in the eighteenth century or earlier). In both cases, the American biota was not yet well described, and, as noted above, these (and no doubt other) species first landed at the feet of European taxonomists. Similarly, the nineteenth century importation of exotic aquatic plants from Asia to the Kew Gardens of England (Desmond 1995) brought as yet undescribed associated species to the attention of British zoologists; examples include the freshwater jellyfish *Craspedacusta sowerbii* (Table 2.4 section B) and the freshwater worm *Branchiura sowerbyi* (Table 2.2).

For both this and the next category, an attendant risk is using a geographic name for a species, especially for taxa from harbors, ports, and other coastal zones influenced by human transport mechanisms (such as the Indian Ocean hydroid *Garveia franciscana*, or the New Zealand isopod *Iais californica*). Species with trivial names such as *californica*, *mexicana*, *mediterraneus*, and so forth, do not easily invite workers to look for the same species to be native on the other side of the world (see also an example from Brazil in Chap. 27, Ferreira et al.).

Admitted to Table 2.2, but an exception relative to the other species treated in this category, is the seaslug *Babakina festiva*. Although first described from California and not recognized as an introduction at the time, Roller (1972) noted that it had been known from Japan since at least 1956.

Unrelated to this phenomenon is the error of bestowing a geographic name on a species based on a mistaken source of the specimens being described. Thus the leucosiid (pebble) crab *Persephona mediterranea* (Herbst 1794) is a Western Atlantic species which does not occur in the Mediterranean (Williams 1984), while the purse oyster *Isognomon californicum* (Conrad, 1837) is a native Hawaiian

species which does not occur in California (Kay 1979). A specimen of the Indo-West Pacific angelfish *Chaetodontophus mesoleucus*, mislabeled as coming from the Hawaiian Islands, was mistakenly redescribed as *Holacanthus bicolor oahuensis* Borodin, 1930 (Mundy 2005).

Category 3: introduced species described as new after introduction, and remaining unknown elsewhere The fewest examples of pseudoindigenes are in this category: if a species is not known from elsewhere, an assumption may be that it is native to the place where it is known. On the other hand, there may be clear but overlooked evidence that a species is not native. Such evidence may include localization to one or a few harbors along a well-explored coastline (perhaps combined with the demonstration that the species was not collected earlier and was not likely to be overlooked in previous centuries, when, in the same locations and habitats, extremely rare native species were collected), species whose only close morphological relatives are in another part of the world, species closely associated with a human transport vector, and so on. As noted elsewhere (Chapman and Carlton 1991, 1994), multiple sets of evidence, rather than relying on any one supporting criterion, strengthen such recognition.

Seven examples are shown in Table 2.3. Species that are restricted to one or a few harbors and are otherwise associated with introduced biotas include the sponge *Halichondria coerulea* and the crab *Pilumnus oahuensis*, both in Hawaii.

Table 2.3 Examples of introduced species described from non-Native regions and remaining unknown elsewhere

Species	Native to	Described from	Reference
Anthozoa (corals)			
Culicia rachelfitzhardingeae Cairns, 2006	Indo-Pacific?	Hawaii	Cairns (2006); Carlton and Eldredge (2009)
Porifera (sponges)			
Halichondria coerulea Bergquist, 1967	Indo-Pacific?	Hawaii	Carlton and Eldredge (2009)
Isopoda (isopods)			
Iais floridana Kensley & Schotte, 1999	Indian Ocean?	Florida	Herein
Caeijaera horvathi Menzies, 1951	Southern hemisphere?	California	Carlton and Eldredge (2009)
Ostracoda (ostracodes)			
Redekea californica De Vos & Stock,1956	Southern hemisphere?	California	Carlton (1979)
Decapoda (crabs)			
Pilumnus oahuensis Edmondson, 1931	Indo-Pacific/tropical East Pacific?	Hawaii	Carlton and Eldredge (2009)
Tunicata (sea squirts)			
Botrylloides diegensis Ritter & Forsyth, 1917	Indo-Pacific?	California	Carlton (2005)

The commensal isopod *Iais floridana*, described from Florida, is regarded as an introduction from the Indo-Pacific: its sole host is the introduced isopod *Sphaeroma terebrans*, and it is a close relative (if not a sibling species) of the Pacific Ocean *Iais singaporensis*.

The California botryllid seasquirt *Botrylloides diegensis*, described in 1917 from harbor pilings in San Diego, California, is regarded as introduced from the Western or South Pacific, where it is predicted it will be discovered. It is part of a clade of *Botrylloides* species all found in the Western or South Pacific; *B. diegensis* has no relatives in the Northeastern Pacific. It is suggested that it was carried in ship fouling to southern California in the nineteenth or earlier centuries.

Described as new, but recognized at the time as introduced Not strictly members of the above three categories are introduced species that while described as new were recognized at the time of description as non-native. Thus, these are not pseudoindigenes, as they were not mistaken as native species. Examples of these, which are presented here as a "tip of the hat" to the systematists and biologists who recognized their species as non-native, are shown in Table 2.4, divided into three categories, that parallel those above: species that were mistakenly redescribed (Table 2.4 section A), species first described from a non-native region and then found elsewhere (Table 2.4 section B), and species described from a non-native region and remaining unknown elsewhere (Table 2.4 section C). These investigators employed a variety of evidence to deduce that the species was not native; this evidence includes prior absence, association with a habitat created by human activity and dominated by exotic biota, and morphological similarity to autochthonous taxa. In the first case (Table 2.4 section A), there is the occasional temptation to describe introduced populations – although recognized as such! – as new subspecies (such as the barnacle *Balanus amphitrite saltonensis*, the amphipod *Caprella acanthogaster humboldtiensis*, the worm *Pseudopolydora kempi californica*, all from California, and all bestowed with regional names).

Cooper (1872), although recognizing the potential for ship-mediated transport of marine organisms, proceeded to describe the marsh snail *Alexia setifer* as a new species from San Francisco Bay, pointing out that the localities where it was found had been searched by collectors "for more than 20 years" prior to its discovery in 1871 – a rather strong assertion for how well those Bay shores were known in the 1850s and 1860s. Although unable to match it with a described Asian species, Cooper speculated that it may have been introduced with ships from China. Less than one year later Cooper (1873) recognized that it was the Atlantic snail *Phytia myosotis* (now *Myosotella myosotis*), although an erroneous reversal of nomenclatural fortune in the 1920s led to the use of the specific name *setifer* once again for the next 30 years.

The Japanese oyster-eating flatworm *Pseudostylochus ostreophagus* was first discovered in Puget Sound, Washington, in beds of imported Japanese oysters (*Crassostrea gigas*). Upon its discovery, fisheries biologists immediately went to Japan and discovered the flatworm there. The description of this worm as a new species was thus based on specimens from its native region (Hyman 1955). It is not listed in any of the tables here. This is a rare instance – and provides an important

Table 2.4 Examples of introduced species recognized at the time of their description as non-native or possibly non-native

A. Introduced species mistakenly redescribed from non-native regions

Species	Native to	Redescribed as (from)	Reference
Turbellaria (flatworms)			
Caenoplana coerulea Moseley, 1877	Australia	*Geoplana vaga* Hyman, 1943 (California)	Ogren (1989b)
Polychaeta (worms)			
Pseudopolydora kempi (Southern, 1921)	Indo-West Pacific	*Pseudopolydora kempi californica* (California)	Radashevsky and Hsieh (2000)
Cirripedia (barnacles)			
Balanus amphitrite Darwin, 1854	Indo-Pacific	*Balanus amphitrite saltonensis* Rogers, 1949 (Salton Sea, California)	Henry and McLaughlin, (1975); Flowerdew (1985); Raimondi (1992)
Amphipoda (amphipods)			
Caprella mutica Schurin, 1935	Japan	*Caprella acanthogaster humboldtiensis* Martin, 1977 (California)	Marelli (1981)
Mysidacea (mysids)			
Hyperacanthomysis longirostris Ii, 1936	Asia	*Acanthomysis bowmani* Modlin & Orsi, 1997 (California)	Fukuoka and Murano (2000)
Gastropoda (snails)			
Myosotella myosotis (Draparnaud, 1801)	Europe	*Alexia setifer* Cooper, 1872 (California)	Cooper (1872); Martins (1996)
Tunicata (sea squirts)			
Eusynstyela hartmeyeri Michaelsen, 1904	Red Sea, Indian Ocean	*Eusynstyela aliena* Monniot, 1991 (New Caledonia)	Monniot and Monniot (2001)

B. Species first described from non-native regions and subsequently found elsewhere

Species	Native to	Described from	Reference
Hydrozoa (hydroids)			
Craspedacusta sowerbii Lankester, 1880	China	Kew Gardens, London	Russell (1953)
Polychaeta (worms)			
Ficopomatus enigmaticus (Fauvel, 1923)	Australia	France	Cohen and Carlton (1995)
Copepoda (copepods)			
Oithona davisae Ferrari & Orsi, 1984	Asia	California	Ferrari and Orsi (1984)

(continued)

Table 2.4 Examples of introduced species recognized at the time of their description as non-native or possibly non-native

Isopoda (isopods)			
Gnorimosphaeroma rayi Hoestlandt, 1969	Japan	California	Hoestlandt (1973)
Bryozoa (bryozoans)			
Watersipora edmondsoni Soule & Soule, 1968	Indo-Pacific	Hawaii	Winston and Heimberg (1986)
C. Species first described from non-native regions and remaining unknown elsewhere			
Species	Native to	Described from	Reference
Turbellaria (flatworms)			
Bdellocephala exotica (Hyman, 1953)	Asia?	Washington, D.C.	Hyman (1953)
Bipalium pennsylvanicum Ogren, 1987	Asia?	Pennsylvania	Ogren (1987)
Anthozoa (sea anemones)			
Diadumene franciscana Hand, 1956	Indo-Pacific/Asia?	California	Cohen and Carlton (1995)
Amphipoda (amphipods)			
Transorchestia enigmatica Bousfield & Carlton, 1969	New Zealand/Chile	California	Bousfield (2007)
Corophium alienense Chapman, 1988	Southeast Asia	California	Chapman (1988)
Mysidacea (mysids)			
Deltamysis holmquistae Bowman & Orsi, 1992	Asia	California	Bowman and Orsi (1992)
Decapoda (crabs)			
Acantholobulus pacificus (Edmondson, 1931)	Tropical Eastern Pacific	Hawaii	Felder and Martin (2003)

lesson in systematic biogeography – of a species being discovered in a non-native region, followed by biologists taking the unusual pro-active step (in this case economically motivated) to discover the origin of the species.

Category 4: introduced species misidentified as previously known native species Introduced species may be misidentified as native species because of insufficient taxonomic resolution, or because, despite seemingly adequate morphological taxonomy, cryptic invasions may occur that can only be revealed genetically.

Imperfect taxonomy Non-native species may be misidentified as described native species; we might say, "similar-looking native species," but such is not always the case. The introduced Atlantic gem clam *Gemma gemma* was misidentified as the quite distinct native Pacific clam *Transennella tantilla* (now *Nutricola tantilla*) throughout the American Pacific Northwest for many years (Carlton 1979). The introduced Atlantic amphipod *Ampelisca abdita* was referred to for many years in

San Francisco Bay as the Pacific amphipod *Ampelisca milleri*, despite the fact that, apart from clear morphological differences, the former occurred in estuarine muds in the Bay, and the latter was described from the open ocean, 75 m offshore of San Miguel Island, in southern California (Chapman 1988). The Japanese snail *Batillaria attramentaria* was misidentified as the native snail *Cerithidea californica* when first found in 1951 in Monterey Bay, California (Carlton 1979).

In more recent and better-known examples, the invasion of the Japanese seastar *Asterias amurensis* in Australia went unnoticed because it was misidentified for some years as the native seastar *Uniophora granulata* (Buttermore et al. 1994), and the first-observed specimens of the Caribbean barnacle *Chthamalus proteus* in Hawaii were identified as the native Hawaiian barnacle *Euraphia hembeli* (Zabin et al. 2007).

It may thus be predicted with some confidence that invasions have gone, or will go, unnoticed because of external morphological resemblances to similar-looking native species. The northeastern Pacific barnacle *Balanus glandula* is now well established in Argentina (Schwindt 2007) and in Japan (Kado 2003), but as a small white "acorn barnacle," may be overlooked elsewhere. Similarly, *Chthamalus proteus*, now abundant in the Hawaiian Islands (Southward et al. 1998) would be a challenge to detect if introduced to the warm coasts of California and Mexico (C. Zabin, personal communication), where other *Chthamalus* species occur. Godwin (2003) has noted that *C. proteus* survives on vessels on round-trip voyages between California and Hawaii.

Cryptic genospecies invasions Cryptic species (Bickford et al. 2007) provide one of the most difficult challenges in recognizing invasions, especially if a new invader appears to be morphologically identical to a native congener. A well-known example is the invasion of the Mediterranean mussel *Mytilus galloprovincialis* in southern California in the mid-twentieth century, which although first believed to be an invasion from Japan, was concluded to be a resurgence of the native mussel *Mytilus trossulus* (then known as *Mytilus edulis*, and specifically described as a new subspecies, *M. edulis diegensis*; Carlton 1979). As Geller (1999) has shown, this "resurgence" consisted of the invasion of the morphologically identical but genetically distinct non-native *M. galloprovincialis*.

In a parallel case, the marsh reed *Phragmites australis* "became" invasive in the nineteenth and twentieth centuries in Eastern North America; the invasion was caused by a non-native (but morphologically similar) genotype of *P. australis* (Saltonstall 2002).

Genetic analyses have also aided in revealing invasions of species of the jellyfish *Aurelia* (Dawson et al. 2005) and *Cassiopeia* (Holland et al. 2004), the polychaete worm *Myrianida* (Nygren 2004), the vermetid snail *Thylaeodus* (Strathmann and Strathmann 2006; Carlton and Eldredge 2009), the freshwater limpet *Ferrissia* (Walther et al. 2006), the bryozoans *Bugula* and *Watersipora* (Mackie et al. 2006), the brittlestar *Ophiactis* (Roy and Spooner 2002), and others. Many more such cases are to be expected.

Unidentified species, including many "cosmopolitan" species In most surveys of fauna and flora (sensu lato) some to many species cannot be identified for many reasons. These taxa should not default to being listed as "native," as is often the case. Thus these species are often not amenable to biogeographic assessment unless

they are demonstrably undescribed taxa recognized as probable endemics to the region based upon habitat (such as deep cave endemics) or related taxa. Lee et al. (2003) refer to unidentified species as "indeterminate taxa." Clearly, introduced species may be amongst these, and perhaps commonly so. As noted above, when evidence can be mustered, some unidentified taxa can be considered cryptogenic, but taxa resolved only to phyletic, class, or ordinal levels should generally be considered as unidentified, and not cryptogenic (as used, for example, by Wasson et al. 2004).

Added to this category would be certain "species" whose only apparently available scientific name is one used for the same, or similar-looking, taxon around the world. These "cosmopolitan" taxa may include (1) species that have been globally spread by ships or other vectors (introductions), (2) a species-complex (including both native – and often undescribed – and introduced species), or (3) conceivably one naturally widespread species, although adequate mechanisms for global gene flow in ecological time that would prevent allopatric speciation are difficult to imagine, especially when no dispersal corridors appear to exist.

Thousands of species groups have not been adequately sorted into one of these three categories, and thus taxa with cosmonames should in many cases simply, but frustratingly, revert to being regarded as unidentified. This strategy would serve to strip away from a number of lists both introduced and cryptogenic species (for example, Cohen and Carlton 1995; Wasson et al. 2004). Marine examples include some "species" in the protist genera *Zoothamnium* and *Vorticella*, the sponge genus *Cliona*, hydroid genera such as *Plumularia, Sertularella, Campanularia*, *Obelia*, *Gonothyraea*, and *Dynamena*, bryozoan genera such as *Bugula* and *Bowerbankia*, and the caprellid amphipod genus *Caprella*.

An immediate derivative of this perspective is that assessments of regional biodiversity should divide all taxa into four categories: native, introduced, cryptogenic, and unidentified.

Small species Many microbial (Finlay 2002; Fenchel and Finlay 2004) and microscopic (Wyatt and Carlton 2002) species – essentially many taxa less than 1 mm in size – are considered naturally cosmopolitan, in part based upon the presumption that global dispersal for small organisms is naturally fluid and continuous, thus preventing allopatric speciation. Arguing against this is that wind and water do not act to homogenize the entire world; recent molecular evidence (Green and Bohannan 2006) thus suggests, not surprisingly, that greater provincial diversity exists among small organisms.

Because of severe taxonomic and biogeographic challenges, including the perception of natural cosmopolitanism noted above, small organisms are reported as introductions far less often than larger organisms. Newly-discovered small organisms– perhaps noticed because they have become common to abundant – are often assumed to be native. This rationale is based in part upon two arguments: (1) previously rare taxa may respond to environmental changes and become abundant (and thus detectable), and (2) new techniques permit the discovery of previously undetectable taxa. Relative to the first case, newly recognized taxa invoked as native were not simply previously rare – they were never previously recorded. In contrast, in most

biotas, many extremely rare species may have been recorded over time. This argument thus requires that the species were so rare as to have survived no previous detection, and had no previous episodes of becoming common or abundant. Relative to the second case, improved microscopic and molecular techniques do permit fine-scale resolution of taxa previously undetectable, but previously undetectable taxa are not by default native – they were simply previously undetectable.

Carlton (in Wyatt and Carlton 2002) referred to this phenomenon as the "smalls rule of invasion ecology," defined as an inverse correlation of body size with the ability to be recognized as non-native (Carlton 2003). Thus small filamentous algae, other protists (such as foraminiferans, rhizopods, actinopods, ciliates, dinoflagellates (including *Pfiesteria* spp.), pelagophyceans (including *Aureococcus* spp.), diatoms, etc.), hydroids, flatworms, small nemerteans, rotifers, gastrotrichs, kinorhynchs, nematodes, oligochaetes, small polychaetes, copepods, mites, bryozoans, and a host of other taxa are rarely reported as invasions.

The same arguments that underlie the principles of natural dispersal of small organisms – ease of transport, the ability to form dormant life stages, large population sizes, and other characteristics (Fenchel and Finlay 2004; Green and Bohannan 2006) – equally support the possibility that many modern-day distributions of small organisms were created by the movement of terrestrial and aquatic media over the past centuries by human activity. Given this, it cannot logically be assumed that only natural dispersal has been in play.

Karling et al. (2000) examined the genetic variation (in the small subunit ribosomal RNA gene) of three species of planktonic foraminiferans that occur in both the Arctic and Antarctic, and identified at least one identical genotype in all three species, "indicating that trans-tropical gene flow must have occurred." Oceanographic phenomena that would lead to such gene flow in ecological time are speculative and have not been clearly demonstrated (Karling et al. 2000). In contrast, there has been clear potential for centuries of transtropical gene flow of planktonic foraminiferans – including between high-latitude waters – by means of steamship bath water in the nineteenth and early twentieth centuries, and by means of ballast water since the nineteenth century and continuing to date. Carlton (1985) has commented on the potential for the interchange of oceanic plankton by such human-mediated means as an alternative hypothesis to natural mixing.

The nearly complete absence of reports of introductions of such prominent planktonic and benthic taxa as diatoms and ciliate "protozoans" may be one of the larger gaps in introduced species diversity assessment. Indeed, in estuarine systems such as San Francisco Bay, it is possible that over 100 species of "protozoans" associated with soft and hard substrates, could be introduced, which, if so, alone would increase by more than one third the known invasions in the Bay. I comment upon the rarity of reports of introduced diatoms below.

Uninvestigated taxa A hallmark of modern censuses of marine life is that there are few or no systematists available to assist in the specialized collection and identification of an increasing number of taxa. The importance of the involvement of taxonomic experts in both field and laboratory work cannot be underestimated. Passive collections – samples taken by others and then provided to a systematist – often miss many small and cryptic taxa. Based upon my experience with "rapid assessment

surveys" – in this case, biological surveys focused on boat harbor fouling communities along the coasts of North America and England – systematists working in the field often recover significantly more species in their specialty than do general field biologists. More importantly, there are often no available systematists in a region or country to assist either with such field work or with the identification of specimens.

Notable dearths in expertise now occur in "protozoans," sponges, hydrozoans, flatworms, nemerteans, nematodes, gastrotrichs, kinorhynchs, rotifers, kamptozoans, tardigrades, "oligochaetes," polychaetes, leeches, ostracodes, copepods, peracarid crustaceans in general (mysids, cumaceans, tanaids, isopods, amphipods), pycnogonids, mites, marine insects, bryozoans, and ascidians. In all of these groups, with regional exceptions, invasions are rarely reported. This category (uninvestigated taxa) overlaps with that of another, undersampled parasitic, commensal, or symbiotic associations, below.

Known but unreported taxa Interviews with systematists, naturalists, local biologists with many years of regional residence, and others, reveal that researchers are frequently aware of unpublished records of introduced species in a given region. Primary reasons cited for not publishing such records are lack of a perceived outlet to publish a paper on a new geographic record of one species, lack of time to write such papers, and, with some museum taxonomists, surprise that there would be interest in a new record of a small or "obscure" species.

2.3 Invader Underestimation – Biogeographic and Community History

2.3.1 Widespread Intraoceanic and Interoceanic Corridor Species

Widespread species within an ocean basin (intraoceanic) and between ocean basins (interoceanic) are almost always interpreted as natural distributions, in place for an undetermined length of time. When corridors are present – coastlines, continental shelves, islands, and so on – the interpretation of such distributions as natural and long-standing appears logical. On the other hand, absent paleontological and archeological evidence, we often have little to no understanding of the aboriginal distributions of many such widespread "corridor" species prior to the onset of global shipping, whose multi-millennial antiquity relative to invasions is clear (di Castri 1989; Leppäkoski et al. 2002; Wolff 2005).

What is the scale of this ancient potential human-mediated homogenization of biota, resulting in biogeographic patterns that mirror presumptive natural patterns? The Indo-Pacific marine biota serve as an example: here, presumably millions of species (most undescribed) occur in shallow waters from the Red Sea to Australasia, and often to outlying island groups, as far as the Hawaiian Archipelago, with less diverse groups reaching as far as the tropical and subtropical Eastern Pacific islands and coastlines. From the 1500s to the 1800s, ocean-going ships were floating zoos

and botanical gardens of entrained species inside and outside their hulls (Carlton 1987, 1999a; Carlton and Ruiz 2003). Carlton (1999a) constructed an "imaginary assemblage of marine organisms on a wooden sailing vessel of 1750," excluding parasites, commensals, and other symbiotic species. Noting the scale of microhabitats available – hull fouling, hull boring, hull nestlers, the anchor, anchor chain, and anchor chain locker, sand and rock ballast – total species richness was calculated as easily over 150 species.

Carlton (1987) noted that this potential for ship-mediated homogenization "throughout the atolls and high islands of the central and South Pacific has rarely been considered." That a great many interoceanic and intraoceanic species had more restricted ranges prior to the onset of shipping – even if corridors were apparently available to such taxa – needs careful examination, a possibility that can now be tested with genetic analysis. In a similar fashion, Carlton and Hodder (1995) have argued that even along a moderately uniform coastline, ships transporting native species for centuries may have obscured original patterns of distribution.

In addition, species introduced to a coastline (or to an archipelago) can, over the centuries, become so widespread as to mimic natural patterns: we are often disinclined to suspect a species' natural status if it occurs from Alaska to Mexico, or from the Bay of Fundy to the Gulf of Mexico. Since many introduced species on these (and all) coasts have easily achieved such wide distributions, latitudinal breadth of occurrence can rarely alone be used to indicate either endemicity or aboriginal distributional patterns: the Asian alga *Neosiphonia harveyi* now ranges from Newfoundland to the Caribbean. Strasser (1999) has also noted that distributions created by human activity in modern time can recreate and parallel ancient distributions: the clam *Mya arenaria* was once widespread through the high latitudes of the North Atlantic and North Pacific Oceans until Pleistocene glaciation eliminated all but the Western North Atlantic populations: it was subsequently introduced (not reintroduced, having never been introduced in the first place) by humans to the Pacific Ocean and to Europe, recreating Tertiary patterns.

2.3.2   Neritic Species with Presumptive Oceanic Dispersal

As noted above, for many taxa there is a presumption that natural dispersal may play the greater role in the distribution of a species, even if such taxa are recorded from ship fouling and are unknown from ocean currents. Orensanz et al. (2002) and Castilla et al. (2005), presenting the first inventories of marine bioinvasions of Uruguay/Argentina, and Chile, respectively, thus excluded from consideration hydromedusae (and their hydroid polyps) and wood borers (such as gribbles, limnoriid isopods) and shipworms (teredinid bivalves), under the argument that their dispersal may also be natural on ocean currents. This will very likely lead to an underestimation of invader biodiversity.

Hydrozoan taxa involved represent harbor-dwelling fouling species in such genera as *Obelia, Campanularia, Sarsia, Ectopleura*, *Pinauay*, and *Plumularia*. Wood-

boring taxa involved live in shallow bays, estuaries, and harbors; these include certain species of shipworms in the genera *Teredo* and *Lyrodus*, and certain species of gribbles in the genus *Limnoria*, known to infest wooden ships for centuries. None of the wood-boring species that are found in estuaries or harbors (or in wooden-hulled vessels), and none of the hydroids (polyps and medusae) found in fouling communities or open waters of marinas, ports, and harbors (or on ships' hulls or in ballast water) have been reported from ocean currents. Carlton (1999b) detailed the arguments, using shipworms as a model, that neritic taxa capable of floating or being floated require discovery in the open ocean before oceanic dispersal can be invoked. Relative to shipworms, the species found in floating wood at sea are, not surprisingly, a guild of neustonic, oceanic species, capable of living in that environment (and, in turn, are not the shipworm species found in harbors and ports).

2.3.3 Resident Species

As noted above, historical invasions are often difficult to detect, albeit less so now with the availability of genetic techniques. Not surprisingly, most invasions in the ocean have been recognized only since marine biologists appeared on the scene, even though vectors such as shipping had been in place for many centuries. Thus, European species were regularly transported to New England (and vice versa) on and in ships from the 1500s and on (and with more episodic earlier Viking voyages 500 years earlier). The documentation of the marine fauna and flora on both sides of the North Atlantic commenced 200–300 years later, in the 1700s and 1800s, with North American animals and plants being shipped back to European biologists for study and naming. Although larger fish, mollusks, and crustaceans reached European cabinets and universities by the late 1600s, most smaller taxa (such as bryozoans, sponges, hydroids, ascidians, small crustaceans, worms, and the remaining plethora of small invertebrates) were not specifically collected and shipped as such. The long history of invasions prior to collectors and biologists being present, combined with the lack of early investigations of many animal and plant groups, set the stage for the presumption of natural amphiatlantic distributions for many shallow-water taxa (Carlton 2003).

Stachowicz et al. (1999, 2002a, b) thus categorize certain fouling ascidians that occur both in Europe and New England as "native" species, including *Ciona intestinalis* and *Botryllus schlosseri*, as well as the fouling bryozoan *Cryptosula pallasiana*, and examine the interaction between these species and the introduced ascidians *Ascidiella aspersa, Diplosoma listerianum*, and *Botrylloides violaceus*. Stachowicz et al. (2002b) note that "Although the true status of the New England sea squirts as natives or invaders is difficult to resolve due to the poor fossil record of these soft-bodied organisms, all of these species have been present in New England for as long as humans have been studying these animals. Thus, these species form the resident community that current invaders encounter upon arrival."

Species status is not a dichotomy of native or introduced, and *Ciona, Botryllus* and *Cryptosula* can be considered cryptogenic, but not native. Genetic investigations will materially aid in sorting out these histories. Van Name (1945) considered *Botryllus schlosseri* to be introduced by ships from Europe to North America, and Carlton (2005) has proposed that it may in fact be native to the southwestern Pacific Ocean. Equally – or more – interesting, of course, is the interaction between a newer set of invaders and a previous set of invaders in terms of community history and development. Regardless, the concept of "resident" or "naturalized" is not a separate or distinct category of biogeographic, ecological, environmental, historical, or evolutionary status. Taxa capable of being identified to the species level are either native, introduced, or cryptogenic.

2.4   Invader Underestimation – Sampling

2.4.1   Species in Underexplored Habitats and Associations

All of the historical and taxonomic challenges noted above are further compounded when attempting to assess the systematics and biogeographic history of parasitic, commensal, and symbiotic organisms associated with either native species or demonstrably introduced taxa. In large part these challenges are rarely addressed since these associated taxa are rarely sampled in standard surveys. Monographic reports of invasions in marine and freshwater habitats from most areas of the world record the occasional parasitic or symbiotic species that were encountered by specialists, but the undersampling of this biotic component may rival the undersampling of microscopic free-living taxa.

   Similarly, "microhabitats" that require specialized techniques, knowledgeable investigators, and experienced systematists, remain largely uninvestigated relative to invasions. Meiofaunal communities are a striking example. Ecotonal habitats, such as the supralittoral fringe (Carlton 2002) or oligohaline zones in estuaries, often have unique assemblages of species, but are the subject of few studies, and fewer still for invasions, as habitat-oriented ecologists often do not find themselves in transitional environments. Thus few terrestrial or marine ecologists have studied the intermediate maritime zone; similarly, freshwater and marine biologists have rarely studied the oligohaline zone between these two habitats.

2.4.2   Incipient Invasions: Species with Small Population Sizes

Newly invading species will, in the early stages of colonization, generally have small and restricted populations that are often difficult to detect through standard sampling programs, unless haphazardly stumbled upon. These are thus initially rare

species, and fall into sampling challenges universal to assessing alpha diversity in a community (Rabinowitz et al. 1986; Chapman 1999). If vectors are present that lead to the continual inoculation (release) of propagules into a system, it is probable that at any given time some species are in the early stages of establishment, and may not be detected until several generations have reproduced. This is one of the most enduring challenges of quickly assessing the efficacy of vector management, as population lag times may lead to the detection of a new invader years after it is thought that a given vector is under some measure of control.

2.5   The Overestimation of Invader Diversity

Miscategorizing native species as introduced is rare, in large part because the classical default in systematics, evolutionary biology, and biogeography, is to assume that a species is native. Galil et al. (2002) note that the alpheid shrimp *Automate branchialis* Holthuis & Gottlie, 1958 was first considered to be a Lessepsian invader, but is in fact native to the Mediterranean Sea. Carlton and Eldredge (2009) note several cases of native Hawaiian mollusks, including *Bulla vernicosa, Vitularia miliaris*, and *Conus capitaneus*, mistaken as invasions. Understandably, based upon previous literature, Calcinai et al. (2004) treat the octocoral *Carijoa riisei* as an Atlantic species introduced to the Indo-Pacific, but it now appears to be native to the Pacific (Kahng 2005).

A classic and more complex case involves the history of the perception of the biogeography of the Atlantic South American xanthid crab *Pilumnoides perlatus* (Poeppig, 1836). Barnard (1950) noted its presence on ship-bottoms in South Africa; combined with its report of having been transported by ships to Britain, he suggested that it might be introduced to South Africa. However, Kensley (1981, p 10) speculated that its presence in both southern South America and in South Africa might be natural, explained by larval transport on the West Wind Drift, but he also believed that the question remained open as to whether it was introduced one way or the other (B. Kensley, personal communication).

Guinot and MacPherson (1987) then showed that the South African species, previously identified as *P. perlatus*, was in fact an undescribed taxon, naming it *Pilumnoides rubus*. In a further complication, they also then described the British specimens as a new native species, *Pilumnoides inglei*, rejecting the idea that it was introduced by ships. In addition to the fact that *P. inglei* had not been collected since 1913, they remarked that it was with "beaucoup d'hesitation que nous avons separe ce Crabe des cotes anglaises sous un nom distinct" [great hesitation that we have separated this crab from the British coasts under a distinct name]. They speculated that perhaps it was a cryptic species ("au biotope sans doute tres particulier" [without doubt a very special habitat]) in an attempt to explain why it had not been rediscovered. They noted it was, however, extremely close to the South American *P. perlatus*; despite describing it as a new species, they further noted that "nous n'avons pas releve de differences vraiment importantes entre ces deux

especes" (!) [we have not noticed any truly important differences between the two species]). Ingle (1997) subsequently treated *P. inglei* as an introduced South American species, where, if it is distinct from *P. perlatus*, it remains unreported. As the systematics remains unsettled, it is not included here in Table 2.3, a category where *P. inglei* may eventually reside, returning to the original hypothesis that it was introduced.

2.6 Discussion

Taken as a whole, the combination of species that are cryptogenic, pseudoindigenous (including cryptic), unidentified, small, uninvestigated, unreported, pseudo-intraoceanic, pseudo-interoceanic, pseudo-oceanic, introduced "resident species," undersampled, and rare, potentially significantly alters our perception of the scale of invasions over time and space.

Perhaps no better examples of this are at hand than six recent independent studies in the Pacific and Atlantic Oceans (Table 2.5), summarizing known invasions in Denmark, the Azores, South Africa, Uruguay/Australia, Japan, and Chile. Each of these countries has experienced global shipping contact for many centuries. Despite the antiquity of external contact, no invasions are recognized in Denmark, Azores, South Africa, or Chile prior to the mid-nineteenth century (no earliest introduction dates are provided in the studies from Uruguay/Australia and Japan). The sole exception is the archeological recognition of the introduction by the Vikings of the North American soft-shell clam *Mya arenaria* to the European theatre in the thirteenth or fourteenth centuries.

Further, despite the potential scale of introductions, only a relatively few invasions are recognized from all of these locations, with a maximum of 33 species from the Azores, ranging down to only 18 in Denmark. In each of the countries shown in Table 2.5, we would expect significantly more invasions, at scales up to 5–10 times the numbers shown. The list of 22 species in South Africa (which has had European and transglobal shipping contact steadily since the 1500s) is rapidly expanding as more information is gathered; only 10 species were listed in the Robinson et al. (2005) publication vs the 22 in Chap. 23, Griffiths et al. Heavily obscured by the dark curtains of antiquity, the uncertainties of biogeographic interpretation, and sitting at the mercy of taxonomy, we simply do not yet know how many introduced species dominate the marine and estuarine environments of most coastlines of the world.

One of the central goals of ecology and evolution studies is to understand the patterns of the diversity, abundance, and distribution of species, and thus how communities came to be structured. Without an understanding of the history of communities, we cannot know the extent to which evolutionary processes have played fundamental roles in precipitating structures currently observed. The elegant summary of phytoplankton dynamics in San Francisco Bay, California, by Cloern and

Table 2.5 Estimates of number of introduced and cryptogenic marine species

Location	Number of introductions	Number of cryptogens	Earliest introduction	Reference
Atlantic Ocean				
Denmark	18	None listed	1895[a]	Jensen and Knudsen (2005)
Azores	33	18	1887	Cardigos et al. (2006)
South Africa	22	18	1955	Robinson et al. (2005); Chap. 23, Griffiths and Robinson
Uruguay/ Argentina	31	46	Not indicated	Orensanz et al. (2002)
Pacific Ocean				
Japan	25	None listed	Not indicated	Otani (2004)
Chile	51	None listed	1864	Castilla et al. (2005); Chap. 26, Castilla and Neill

[a] Except for the North American clam *Mya arenaria*, introduced circa 1250–1300

Dufford (2005) provides an example of the potential importance of understanding the history of invasions.

Cloern and Dufford (2005) report 500 distinct phytoplankton taxa in San Francisco Bay, with 396 of these identified to species level. The 81 most important species (by biomass) consist of a "community of cosmopolitan phytoplankton commonly observed in temperate estuaries and coastal waters globally," and "many key phytoplankton species in San Francisco Bay are the same taxa that develop blooms in the adjacent coastal upwelling systems, sugesting that phytoplankton diversity inside the estuary is influenced by exchanges with the coastal Pacific Ocean." Despite the predominance of phytoplankton in ballast water (McCarthy and Crowder 2000; Hulsman and Galil 2002), and despite the number of other additional vectors that have transported benthic diatoms to San Francisco Bay, no introduced diatoms, dinoflagellates, or other phytoprotists are recognized in San Francisco Bay, at either the morphospecies or genospecies level. Whether the presumably endemic coastal taxa informing San Francisco Bay populations are genetically the same as the estuarine taxa has by and large apparently not been established, although Cloern and Dufford (2005) note that "one mode of resilience to environmental variability is the occurrence within morphospecies of genetically distinct strains" (such as, we add here, might be introduced to estuarine environments). That diatoms in the open coastal zone can also be introduced is illustrated by the invasion of the (Australasian?) surf diatom *Attheya armatus* (= *Chaetoceros armatum*) around 1950 into the Pacific Northwest of North America (Schaefer and Lewin 1984).

Cloern and Dufford (2005) note that "phytoplankton photosynthesis is the primary energy supply to metazoan food webs of San Francisco Bay," and that growth and fecundity of invertebrates are strongly correlated with the HUFA (highly unsaturated fatty acids) of their food, particularly eicosapentaenoic acid (EPA) and docosahexaenoic acid (DHA). They note that 17 species comprise 89% of the phytoplankton biomass in the Bay, including two diatoms, two dinoflagellagtes, two cryptophytes, and *Mesodinium rubrum*; in combination these are rich in DHA and EPA and thus "the phytoplankton in San Francisco Bay are of high nutritional quality." Since the biogeographic history of the phytoflora of the Bay is unknown, whether this is a natural situation remains unknown.

In addition, phytoplankton size structure "influences energy allocation between the competing benthic and pelagic food webs because of differences in size-selective feeding between benthic suspension feeders (e.g. bivalve mollusks) and crustacean zooplankton (e.g. calanoid copepods)". Here again, which phytoplankters that contribute to the size spectrum in the Bay are or may be introduced is not known, so that any changing balance struck in influencing energy allocation over the decades is also not known. In turn it may be noted that a large proportion of the benthic suspension feeding community is composed of known introduced species in the Bay.

Cloern and Dufford (2005) further note that "92% of the [phytoplankton] biomass in San Francisco Bay comes from two algal divisions (diatoms and dinoflagellates) in which spore or cyst production is common" – benthic stages being a "mechanism to retain a species' genome within strongly advective systems such as estuaries." Cloern and Dufford (2005) suggest that this retentive mechanism may explain the predominance of cyst-forming species in the Bay – in turn, it may also explain the success of many of these species if they are introduced.

It seems clear that, in the absence of a phytoplankton history of the Bay, and given the fundamental role of phytoplankton in structuring estuarine trophodynamics, if a number of the species of abundant diatoms in San Francisco Bay were not there 100 years ago, a remarkble conversion in energy flow has occurred. While we use phytoplankton communities as a model here for the scale of what may have changed, the principles apply to all taxa, from bacteria to fish.

Carlton (2000, 2003), using the phrase the "Missing 1000," noted that the combination of shipping history and the lack of historical records in many parts of the world could have led to "nearly 1000 coastal species" being early introductions that have been overlooked and are now regarded as native: the late (1990s) recognition of the Asian alga *Neosiphonia harveyi* on the American Atlantic coast (there since the 1840s or earlier), and the even more recent discovery that the "Caribbean" octocoral *Carijoa riisei* (in the Atlantic since the 1850s or earlier) is native to the Indo-Pacific, only serve to underscore the scale at which such invasions may have occurred 100, 200, or more years ago. In retrospect, the number 1000 now seems too low, when the full suite of the sources of error in estimating non-native species is taken into account.

Ubi sumus? (Where are we?) Historical and continuing invasions preclude community equilibrium. In general, despite the number of macroinvasions that most

marine ecologists are aware of around the world, the general sense of both the ubiquity and potential of invasions, and their consequences, appear to remain "off the radar" as a general principle in marine biogeography and community ecology. Thus reports seemingly as simple as a newly discovered amphipod, *Jassa marmorata*, on the Uruguay and Argentinean coast (Alonso de Pina 2005) are made without reference to the possibility of introduction, and yet *J. marmorata* is a potentially important predator structuring communities (Armsby and Tisch 2006). *J. marmorata* now occurs, distributed by ships over centuries, in many regions of the world (Conlan 1990), and yet there are no reports of its role outside the North Atlantic Ocean, because no ecological or experimental studies outside of its native region have been conducted – exactly the type of non-report that has led not a few recent investigators to conclude that most invasions have little to no impact in the communities to which they are introduced. *Ubi sumus*?, indeed.

2.7 The Way Forward: Solutions

Despite the erosion of systematic resources, in terms of the declining availability of taxonomic expertise, there are solutions. In the description of new species or the re-evaluation of old species, eyebrows need to be arched more highly to encompass all known global species within the genus or family of concern, even those from the most distant shores. Such action will reveal that newly-encountered species may well have names elsewhere; hints to potential source regions may arise from a having a finger on the pulse of the diversity and origin of the vectors in one's region that would import non-indigenous species. Re-examination of highly-localized, "endemic" species, especially in urbanized estuaries, will reveal that some of these are redescriptions of species from far-flung corners of the world.

Materially aiding in this endeavor is the application of molecular genetics. Morphological analyses remain the "bread and butter" of identifying species, as laboratories that would undertake genetic studies are not available to or affordable by all. However, genetic techniques in the twenty-first century will become less expensive and will more universally supplement (but not supplant) morphological studies, and we will thus expect significant breakthroughs in assessing both local and global biodiversity, as well as the biogeographic origins of species.

Finally, as a working rule, fewer assumptions should be made about the endemic or indigenous status of species, regardless of their apparently "natural" wide distribution, their size, or their presumptive methods of "natural" dispersal. Being more receptive to the potential scale of biogeographic complications that humans have wrought upon the Earth, long before biologists were present to observe the seeds of change, may reveal the depth and breadth of biotic transformations that commenced many centuries ago.

References

Abbott DP, Johnson JV (1972) The ascidians *Styela barnharti, S. plicata, S. clava*, and *S. montereyensis* in Californian waters. Bull S Calif Acad Sci 71:95–105

Ahyong ST (2001) Revision of the Australian Stomatopod Crustacea. Rec Aust Mus Suppl 26:1–326

Alonso de Pina GM (2005) A new species of *Notopoma* Lowry & Bernard, 1996, and a new record of *Jassa marmorata* Holmes, 1903, from the southwestern Atlantic (Amphipoda: Corophiidea: Ischyroceridae). Proc Biol Soc Wash 118:528–538

Armsby M, Tisch N (2006) Intraguild predation and cannibalism in a size-structured community of marine amphipods. J Exp Mar Biol Ecol 333:286–295

Banse K (1972) On some species of Phyllodocidae, Syllidae, Nephtyidae, Goniadidae, Apistobranchidae, and Spionidae (Polychaeta) from the northeast Pacific Ocean. Pac Sci 26:191–222

Barnard KH (1950) Descriptive catalogue of South African decapod Crustacea (crabs and shrimps). Ann S Afr Mus 38:1–837

Bax N, Carlton JT, Mathews-Amos A, Haedrich RL, Howarth FG, Purcell JE, Rieser A, Gray A (2001) The control of biological invasions in the world's oceans. Conserv Biol 15:1234–1246

Bickford D, Lohman D, Sodhi NS, Ng PKL, Meier R, Winker K, Ingram KK, Das I (2007) Cryptic species as a window on diversity and conservation. Trends Ecol Evol 22:148–155

Bigley RE, Barreca JL (1982) Evidence for synonymizing *Zostera americana* den Hartog with *Zostera japonica*. Aschers Graebn Aquat Bot 14:349–356

Blake JA, Maciolek NA (1987) A redescription of *Polydora cornuta* Bosc (Polychaeta: Spionidae) and designation of a neotype. Bull Biol Soc Wash 7:11–15

Boudry PS, Heurtebise B, Collet F, Cornette, Gerard A (1998) Differentiation between populations of the Portuguese oyster, Crassostrea angulata (Lamarck) and the Pacific oyster, Crassostrea gigas (Thunberg), revealed by mtDNA RFLP analysis. J Exp Mar Biol Ecol 226:279–291

Bousfield EL (1973) Shallow-water gammaridean Amphipoda of New England. Cornell Univ Press, Ithaca New York

Bousfield EL (2007) Amphipoda: Gammaridea: Talitridae. In: Carlton J (ed) The Light & Smith manual: intertidal invertebrates from central California to Oregon, edn 4. University of California Press, Berkeley Los Angeles

Bowman TE, Orsi JJ (1992) *Deltamysis holmquistae*, a new genus and species of Mysidacea from the Sacramento – San Joaquin estuary of California (Mysidae: Mysinae: Heteromysini). Proc Biol Soc Wash 105:733–742

Briggs EA (1931) Notes on Australian athecate hydroids. Rec Aust Mus 18:279–282

Broom JE, Nelson WA, Yarish C, Jones WA, Aguilar Rosas R, Aguilar Rosas LE (2002) A reassessment of the taxonomic status of *Porphyra suborbiculata*, *Porphyra carolinensis* and *Porphyra lilliputiana* (Bangiales, Rhodophyta) based on molecular and morphological data. Eur J Phycol 37:227–235

Buitendijk AM, Holthuis LB (1949) Note on the Zuiderzee crab *Rhithropanopeus harrisii* (Gould) subspecies *tridentatus* (Maitland). Zool Meded 30:95–106

Butman CA, Carlton JT, Palumbi SR (1995) Whaling effects on deep-sea biodiversity. Conserv Biol 9:462–464

Buttermore RE, Turner E, Morrice E, Morrice MG (1994) The introduced Northern Pacific seastar *Asterias amurensis* in Tasmania. Mem Queensl Mus 36:21–25

Byers JE, Reichard S, Randall J, Parker I et al. (2002) Directing research to reduce the impacts of nonindigenous species. Conserv Biol 16:630–640

Cadotte MW, McMahon SM, Fukami T (eds) (2006) Conceptual ecology and invasion biology: reciprocal approaches to nature. Springer, Dordrecht

Cairns SD (2006) New records of azooxanthellate Scleractinia from the Hawaiian Islands. BP Bishop Mus Occas Pap 87:45–53

Calcinai B, Bavestrello G, Cerrano C (2004) Dispersal and association of two aliens species in the Indonesian coral reefs: the octocoral *Carijoa riisei* and the demosponge *Desmapsamma anchorata*. J Mar Biol Assoc UK 84:937–941

Calman WT (1921) Notes on marine wood-boring animals – II. Crustacea. Proc Zool Soc London 1920:215–220

Cardigos FT, Tempera S, Avila J, Goncalves A, Colaco, Santos RS (2006) Non-indigenous species of the Azores. Helgoland Mar Res 60:160–169

Carlton JT (1979) History, biogeography, and ecology of the introduced marine and estuarine invertebrates of the Pacific coast of North America. PhD dissertation, 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 (1987) Patterns of transoceanic marine biological invasions in the Pacific Ocean. Bull Mar Sci 41:452–465

Carlton JT (1992) Introduced marine and estuarine mollusks of North America: an end-of-the-20th-century perspective. J Shellfish Res 11:489–505

Carlton JT (1996) Biological invasions and cryptogenic species. Ecology 77:1653–1655

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

Carlton JT (1999b) Molluscan invasions in marine and estuarine communities. Malacologia 41:439–454

Carlton JT (2000) Quo Vadimus Exotica Oceanica?: marine bioinvasion ecology in the twenty-first century. In: Pederson J (ed) Marine bioinvasions: Proceedings of the First National Conference. Massachusetts Institute of Technology, MIT Sea Grant College Program, MITSG 00-2, Cambridge, Massachusetts, pp 6–23

Carlton JT (2002) Bioinvasion ecology: assessing invasion impact and scale. In: Leppäkoski E, Gollasch S, Olenin S (eds) Invasive aquatic species of Europe. Distribution, impacts, and management. Kluwer Academic Publishers, Dordrecht, The Netherlands, pp 7–19

Carlton JT (2003) Community assembly and historical biogeography in the North Atlantic Ocean: the potential role of human-mediated dispersal vectors. Hydrobiologia 503:1–8

Carlton JT (2005) Setting ascidian invasions on the global stage. Keynote Address, 2005 International Invasive Sea Squirt Conference. Woods Hole Oceanographic Institution, Woods Hole MA. Abstract: http://www.whoi.edu/page.do?pid=11421&tid=282&cid=16303 (accessed April 2007)

Carlton JT, Cohen AN (2003) Episodic global dispersal in shallow water marine organisms: the case history of the European shore crabs *Carcinus maenas* and *Carcinus aestuarii*. J Biogeogr 30:1809–1820

Carlton JT, Hodder J (1995) Biogeography and dispersal of coastal marine organisms: experimental studies on a replica of a 16th-century sailing vessel. Mar Biol 121:721–730

Carlton JT, Eldredge LG (2009). Marine bioinvasions of Hawai'i: the introduced and cryptogenic marine and estuarine animals and plants of the Hawaiian archipelago. Bishop Museum Press, Honolulu, Hawaii

Carlton JT, Ruiz GM (2003) The magnitude and consequences of bioinvasions in marine ecosystems: implications for conservation biology. In: Norse EA, Crowder LB (eds) Marine conservation

biology: the science of maintaining the sea's biodiversity. Island Press, Washington, DC, pp 123–148

Carlton JT, Ruiz GM (2005) Vector science and integrated vector management in bioinvasion ecology: conceptual frameworks. In: Mooney HA, Mack RN, McNeely JA, Neville LE, Schei PJ, Waage JK (eds) Invasive alien species: a new synthesis**.** Island Press, Covelo, California, pp 36–58

Castilla JC, Uribe M, Bahamonde N, Clarke M, Desqueyroux-Faundez R, Kong I, Moyano H, Rozbaczylo N, Santelices B, Valdovinos C, Zavala P (2005) Down under the southeastern Pacific: marine non-indigenous species in Chile. Biol Invas 7:213–232

Chapman JW (1988) Invasions of the northeast Pacific by Asian and Atlantic gammaridean amphipod crustaceans, including a new species of *Corophium*. J Crust Biol 8:364–382

Chapman JW (2007) Gammaridean amphipods. In: Carlton JT (ed) The Light & Smith manual: intertidal invertebrates from central California to Oregon, edn 4. University of California Press, Berkeley Los Angeles

Chapman JW, Carlton JT (1991) A test of criteria for introduced species: the global invasion by the isopod *Synidotea laevidorsalis* (Miers, 1881). J Crust Biol 11:386–400

Chapman JW, Carlton JT (1994) Predicted discoveries of the introduced isopod *Synidotea laevi-dorsalis* (Miers, 1881). J Crust Biol 14:700–714

Chapman MG (1999) Are there adequate data to assess how well theories of rarity apply to marine invertebrates? Biodivers Conserv 8:1295–1318

Clench WJ, Turner RD (1948) The genus *Truncatella* in the Western Atlantic. Johnsonia 2:149–164

Cloern JE, Dufford R (2005) Phytoplankton community ecology: principles applied in San Francisco Bay. Mar Ecol Progr Ser 285:11–28

Coan EV (1979) Recent Eastern Pacific species of the crassatellid bivalve genus *Crassinella*. Veliger 22:1–11

Coan EV, Scott PV, Bernard FR (2000) Bivalve seashells of western North America. Marine bivalve mollusks from Arctic Alaska to Baja California. St Barbara Mus Nat Hist Monogr 2

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. A report for the United States Fish and Wildlife Service, Washington, D.C., and The National Sea Grant College Program, Connecticut Sea Grant, NTIS Rep PB96-166525

Collin R (2000) Phylogeny of the *Crepidula plana* (Gastropoda: Calyptraeidae) cryptic species complex in North America. Can J Zool 78:1500–1514

Conlan KE (1990) Revision of the crustacean amphipod genus *Jassa* Leach (Corophioidea: Ischyroceridea). Can J Zool 68:2031–2075

Cooke WJ (1977) Order Hydroida. In: Devaney DM, Eldredge LG (eds) Reef and shore fauna of Hawaii, Sect 1: Protozoa through Ctenophora. BP Bishop Museum Special Publication 64(1). Bishop Museum Press, Honolulu, Hawaii, pp 71–104

Cookson LJ (1991) Australasian species of Limnoriidae (Crustacea: Isopoda). Mem Mus Victoria 52:137–262

Cooper JG (1872) On new Californian Pulmonata. Proc Acad Nat Sci Phil 24:143–154

Cooper JG (1873) Note on *Alexia setifer* and its allies. Proc Calif Acad Sci Ser 1, 6:14–27

Cornelius PFS (1975) The hydroid species of *Obelia* (Coelenterata, Hydrozoa: Campanulariidae), with notes on the medusa stage. Bull Brit Mus Nat Hist 28:249–293

Cowie RH (1997) Catalog and bibliography of the nonindigenous nonmarine snails and slugs of the Hawaiian Islands. Bishop Mus Occas Pap 50

Cowie RH (1998) Patterns of introduction of non-indigenous non-marine snails and slugs in the Hawaiian Islands. Biodivers Conserv 7:349–368

Darling JA, Reitzel AM, Finnerty JR (2004) Regional population structure of a widely introduced estuarine invertebrate: *Nematostella vectensis* Stephenson in New England. Mol Ecol 13:2969–2981

Dawson MN, Gupta AS, England MH (2005) Coupled biophysical global ocean model and molecular genetic analyses identify multiple introductions of cryptogenic species. Proc Natl Acad Sci 102:11968–11973

Desmond R (1995) Kew: a history of the Royal Botanic Gardens. The Harvill Press, London, 466 pp

di Castri F (1989) History of biological invasions with special emphasis on the Old World. In: Drake JA, Mooney HA, di Castri F et al. (eds) Biological invasions. A global perspective. Wiley, New York, pp 1–30

Edwards C (1976) A study in erratic distribution: the occurrence of the medusa *Gonionemus* in relation to the distribution of oysters. Adv Mar Biol 14:251–284

Emschermann P (1987) Creeping propagation stolons – an effective propagation system of the freshwater entoproct *Urnatella gracilis* Leidy (Barentsiidae). Arch Hydrobiol 108:439–448

Englund RA (2002) The loss of native biodiversity and continuing nonindigenous species introductions in freshwater, estuarine, and wetland communities of Pearl Harbor, Oahu, Hawaiian Islands. Estuaries 25:418–430

Englund RA, Preston DJ, Wolff R, Coles SL, Eldredge LG, Arakai K (2000) Biodiversity of freshwater and estuarine communities in lower Pearl Harbor, Oahu, Hawaii with observations on introduced species. Bishop Mus Tech Rep 16

Felder DL, Martin JW (2003) Establishment of a new genus for *Panopeus bermudensis* Benedict & Rathbun, 1891, and several other xanthoid crabs from the Atlantic and Pacific oceans (Crustacea: Decapoda: Xanthoidea). Proc Biol Soc Wash 116:438–452

Fenchel T, Finlay BJ (2004) The ubiquity of small species: patterns of local and global diversity. Bioscience 54:777–784

Ferrari FD, Orsi JJ (1984) *Oithona davisae*, new species, and *Limnoithona sinensis* (Burckhardt, 1912) from the Sacramento-San Joaquin Estuary, California. J Crustac Biol 4:106–126

Finlay BJ (2002) Global dispersal of free-living microbial eukaryote species. Science 296:1061–1063

Flowerdew MW (1985) Indices of genetic identity and distance in three taxa within the *Balanus amphitrite* Darwin complex (Cirripedia, Thoracica). Crustaceana 49:7–15

Freeman AS, Byers JE (2006) Divergent induced responses to an invasive predator in marine mussel populations. Science 313:831–833

Fukuoka K, Murano M (2000) *Hyperacanthomysis*, a new genus for *Acanthomysis longirostris* Ii, 1936, and *A. brevirostris* Wang & Liu, 1997 (Crustacea: Mysidacea: Mysidae). Plankton Biol Ecol 47:122–128

Galil B, Froglia C, Noel P (2002) CIESM Atlas of exotic species in the Mediterranean. Crustaceans. Decapods and stomatopods. CIESM Publishers, Monaco

Geller JB (1999) Decline of a native mussel masked by sibling species invasion. Conserv Biol 13:661–664

Godwin LS (2003) Hull fouling of maritime vessels as a pathway for marine species invasions to the Hawaiian Islands. Biofouling 19(Suppl):123–131

Gosliner TM, Behrens DW (2006) Anatomy of an invasion: systematics and distribution of the introduced opisthobranch snail, *Haminoea japonica* Pilsbry, 1895 (Gastropoda: Opisthobranchia: Haminoeidae). Proc Calif Acad Sci (4) 57:1003–1010

Green J, Bohannan BJM (2006) Spatial scaling of microbial biodiversity. Trend Ecol Evol 21:501–507

Grosholz ED (2002) Ecological and evolutionary consequences of coastal invasions. Trend Ecol Evol 17:22–27

Grosholz ED (2005) Recent biological invasion may hasten invasional meltdown by accelerating historical introductions. Proc Natl Acad Sci 102:1088–1091

Guinot D, MacPherson E (1987) Revision du genre Pilumnoides Lucas, 1844, avec description de quatre especes nouvelles et creation de Pilumnoidinae subfam. nov. (Crustacea Decapoda Brachyura). Bull Mus Nat Hist Nat Paris (4) 9:211–247

Guiry M (2003) *Neosiphonia harveyi* (J Bailey). http://www.algaebase.org/ (accessed April 2007)

Henry DP, McLaughlin PA (1975) The barnacles of the *Balanus amphitrite* complex (Cirripedia, Thoracica). Zool Verh 141:254

Hoestlandt H (1973) Presence de *Gnorimosphaeroma rayi* Hoestlandt (Isopode, flabellifere) sur les cotes du Japon, de Siberie orientale et d'Hawaii, ainsi qu'indications sommaires de son polychromatisme genetique. C R Acad Sci Paris (D) 276:2817–2820

Holland BS, Dawson MN, Crow GL, Hofmann DK (2004) Global phylogeography of *Cassiopea* (Scyphozoa: Rhizostomeae): molecular evidence for cryptic species and multiple invasions of the Hawaiian Islands. Mar Biol 145:1119–1128

Hulsman N, Galil BS (2002) Protists – a dominant component of the ballast-transported biota. In: Leppäkoski ES, Gollasch, Olenin S (eds) Invasive aquatic species of Europe: distribution, impacts, and management. Kluwer Academic Publishers, Dordrecht, pp 20–27

Huvet AS, Lapègue A, Magoulas, Boudry P (2000) Mitochondrial and nuclear DNA phylogeography of *Crassostrea angulata*, the Portuguese oyster endangered in Europe. Conserv Genet 1:251–262

Huvet A, Fabioux C, McCombie H, Lapègue S, Boudry P (2004) Natural hybridization between genetically differentiated populations of *Crassostrea gigas* and *C. angulata* highlighted by sequence variation in flanking regions of a microsatellite locus. Mar Ecol Prog Ser 272:141–152

Hyman LH (1953) North American triclad Turbellaria. 14. A new, probably exotic, dendrocoelid. Am Mus Novit 1629:6

Hyman LH (1955) The polyclad flatworms of the Pacific coast of North America: additions and corrections. Am Mus Novit 1704:4–7

Ingle RW (1997) Crayfishes, lobsters, and crabs of Europe: an illustrated guide to common and traded species. Springer, Berlin Heidelberg New York

Jass J, Klausmeier B (2000) Endemics and immigrants: North American terrestrial isopods (Isopoda, Oniscidea) north of Mexico. Crustaceana 73:771–799

Jensen KR, Knudsen J (2005) A summary of alien marine benthic invertebrates in Danish waters. Oceanol Hydrobiol Stud 34(Suppl 1):137–162

Kado R (2003) Invasion of Japanese shores by the NE Pacific barnacle *Balanus glandula* and its ecological and biogeographical impact. Mar Ecol Prog Ser 249:199–206

Kahng S (2005) The invasion of a tropical coral reef ecosystem by an alien octocoral, *Carijoa riisei*. Fourth International Conference on Marine Bioinvasions, August 2005, Wellington, New Zealand, p 142 (Abstract)

Karling KF, Wade CM, Stewart IA, Kroon D, Dingle R, Brown AJL (2000) Molecular evidence for genetic mizing of Arctic and Antarctic subpolar populations of planktonic formanifers. Nature 400:43–47

Kay EA (1979) Hawaiian marine shells. Reef and shore fauna of Hawaii. Sect 4: Mollusca. B P Bishop Mus Spec Publ 64

Keen AM (1971) Sea shells of tropical west America; marine mollusks from Baja California to Peru, 2nd edn. Stanford University Press, Stanford, California

Kensley B (1981) On the zoogeography of southern African decapod Crustacea, with a distributional checklist of the species. Smith Contrib Zool 338:64

Kensley B, Schotte M (1999) New records of isopods from the Indian River Lagoon, Florida (Crustacea: Peracarida). Proc Biol Soc Wash 112:695–713

Kimura TM, Tabe M, Shikano Y (1999) *Limnoperna fortunei kikuchiii* Habe, 1981 (Bivalvia: Mytilidae) is a synonym of *Xenostrobus securis* (Lamarck, 1819): introduction into Japan from Australia and/or New Zealand. Venus 58:101–117

Knight-Jones P, Knight-Jones EW, Kawahara T (1975) A review of the genus *Janua*, including *Dexiospira* (Polychaeta: Spirorbidae). Zool J Linn Soc 56:91–129

Kolar CS, Lodge DM (2001) Progress in invasion biology: predicting invaders. Trends Ecol Evol 16:199–204

Kornicke LS (1967) A study of three species of *Sarsiella* (Ostracoda: Myodocopa). Proc U S Nat Mus 122, no 3594

Kott P (1985) The Australian Ascidiacea. Part 1, Phlebobranchia and Stolidobranchia. Mem Qd Mus 23:1–440

Kott P (1998) Tunicata. Zoological catalogue of Australia 34:51–252

Kott P (2004) A new species of *Didemnum* (Ascidiacea, Tunicata) from the Atlantic coast of North America. Zootaxa 732:1–10

Kozloff EN (1946) Studies on the ciliates of the family Ancistrocomidae Chatton and Lwoff (order Holotricha, suborder Thigmotricha). III. *Ancistrocoma pelseneeri* Chatton and Lwoff, *Ancistrocoma dissimilis* sp. nov., and *Hypocomagalma pholadidis* sp. nov. Biol Bull 91:189–199

Kramp PL (1961) Synopsis of the Medusae of the world. J Mar Biol Assoc U K 40

Kronberg I (1986) Riesenchromosomen und Artareal einer baltischen *Telmatogeton* – Art (Diptera: Chironomidae: Telmatogetoninae). Z Zool Syst Evolut 24:190–197

Lapegue S, Batista FM, Heurtebise S, Yu Z, Boudry P (2004) Evidence for the presence of the Portuguese oyster, *Crassostrea angulata*, in northern China. J Shellfisheries Res 23:759–764

Lee H, 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

Leppäkoski E, Gollasch S, Olenion S (eds) (2002) Invasive aquatic species of Europe: distribution, impacts, and management. Kluwer Academic Publishers, Dordrecht

Lockwood JL, Hoopes MF, Marchetti MP (2007) Invasion ecology. Blackwell Publishing, Oxford

Lotze HK, Lenihan HS, Bourque BJ et al. (2006) Depletion, degradation, and recovery potential of estuaries and coastal seas. Science 312:1806–1809

Mackie JA, Keough MJ, Christidis L (2006) Invasion patterns inferred from cytochrome oxidase I sequences in three bryozoans, *Bugula neritina, Watersipora subtorquata*, and *Watersipora arcuata*. Mar Biol 149:285–295

Manuel RL (1988) British Anthozoa (Coelenterata: Octocorallia and Hexacorallia): keys and notes for the identification of the species, edn 2. Synopses of the British fauna (new series), no 18. Linnean Society of London

Marceniuk AP, Ferraris CJ Jr (2003) Ariidae (sea catfishes). In: Reis RE, Kullander SO, Ferraris CJ Jr (eds) Checklist of the freshwater fishes of South and Central America. Porto Alegre: EDIPUCRS, Brasil, pp 447–455

Marelli DC (1981) New records for Caprellidae in California. Proc Biol Soc Wash 94:654–662

Marelli DC, Gray S (1983) Conchological descriptions of *Mytilopsis sallei* and *Mytilopsis leucophaeata* of the brackish Western Atlantic. Veliger 25:185–193

Martins AMF (1996) Anatomy and systematics of the Western Atlantic Ellobiidae (Gastropoda: Pulmonata). Malacologia 37:163–332

McCarthy HP, Crowder LB (2000) An overlooked scale of global transport: phytoplankton species richness in ships' ballast water. Biol Invas 2:321–322

McIvor L, Maggs CA, Provan J, Stanhope MJ (2001) rbcL sequences reveal multiple cryptic introductions of the Japanese red alga *Polysiphonia harveyi*. Mol Ecol 10:911–919

McKoy JL (1975) Further records of *Teredicola typicus* C.B. Wilson, 1942 (Copepoda Cyclopoida) from shipworms in northern New Zealand. N Z J Mar Freshwater Res 9:417–421

Millar RH (1970) British ascidians. Synopses of the British fauna (new series), no 1. Linnean Society of London

Mills CE, Sommer F (1995) Invertebrate introductions in marine habitats: two species of hydromedusae (Cnidaria) native to the Black Sea, *Maeotias inexspectata* and *Blackfordia virginica*, invade San Francisco Bay. Mar Biol 122:279–288

Mobberley DG (1956) Taxonomy and distribution of the genus Spartina. Iowa State Coll J Sci 30:471–574

Modlin RF, Orsi JJ (1997) *Acanthomysis bowmani,* a new species, and *A. aspera* Ii, Mysidacea newly reported from the Sacramento-San Joaquin Estuary, California (Crustacea: Mysidae). Proc Biol Soc Washington 110:439–446

Monniot F, Monniot C (2001) Ascidians from the tropical western Pacific Ocean. Zoosystema 23:201–383

Monniot C, Monniot F, Griffiths CL, Schleyer M (2001) South African ascidians. Ann S A Mus 108

Mooney HA, Cleland EE (2001) The evolutionary impact of invasive species. Proc Natl Acad Sci 98:5446–5451

Morton B (1981) The biology and functional morphology of *Mytilopsis sallei* (Recluz) (Bivalvia: Dreissenacea) fouling Visakhapatnam Harbour, Andhra Pradesh, India. J Moll Stud 47:25–42

Mosely HN (1878) Description of a new species of land-planarian from the hothouses at Kew gardens. Ann Mag Nat Hist Ser 5 1:237–239

Mundy BC (2005) Checklist of the fishes of the Hawaiian Archipelago. Bishop Mus Bull Zool 6

Newman WA, Ross A (1976) Revision of the balanomorph. barnacles: including a catalog of the species. Mem San Diego Soc Nat Hist 9:1–108

Newman WA, Killingley JS (1985) The north-east Pacific intertidal barnacle *Pollicipes polymerus* in India? A biogeographical enigma elucidated by ^{18}O fractionation in barnacle calcite. J Nat Hist 19:1191–1196

Nygren A (2004) Revision of Autolytinae (Syllidae: Polychaeta). Zootaxa 680

Odlaug TO (1946) The effect of the copepod, *Mytilicola orientalis* upon the Olympia oyster, *Ostrea lurida*. Trans Am Microsc Soc 65:311–317

Ó Foighil DO, Gaffney PM, Hilbish TJ (1995) Differences in mitochondrial 16S ribosomal gene sequences allow discrimination among American [*Crassostrea virginica* (Gmelin)] and Asian [*C. gigas* (Thunberg) *C. ariakensis* Wakiya] oyster species. J Exp Mar Biol Ecol 192:211–220

Ó Foighil D, Gaffney PM, Wilbur AE, Hilbish TJ (1998) Mitochondrial cytochrome oxidase I gene sequences support an Asian origin for the Portuguese oyster, *Crassostrea angulata*. Mar Biol 131:497–503

Ogren RE (1984) Exotic land planarians of the genus *Bipalium* (Platyhelminthes: Turbellaria) from Pennsylvania and the Academy of Natural Sciences, Philadelphia. Proc Penn Acad Sci 58:193–201

Ogren RE (1987) Description of a new three-lined land planarian of the genus *Bipalium* (Turbellaria: Tricladida) from Pennsylvania, USA Trans Am Microsc Soc 106:21–30

Ogren RE (1989a) Identification features of the two-lined land planarian *Rhynchodemus sylvaticus*, with evidence that *Rhynchodemus americanus* is conspecific. Trans Am Microsc Soc 108:40–44

Ogren RE (1989b) Redescription and a new name for the blue land planarian *Geoplana vaga* Hyman now considered conspecific with *Caenoplana coerulea* Moseley from Australia (Turbellaria: Tricladida: Geoplanidae). J Penn Acad Sci 63:135–142

Orensanz JM, Schwindt E, Pastorino G et al. (2002) No longer the pristine confines of the world ocean: a survey of exotic marine species in the southwestern Atlantic Ocean. Biol Invas 4:115–143

Otani M (2004) Introduced marine organisms in Japanese coastal waters, and the processes involved in their entry. Jpn J Benthol 59:45–57 (English abstract, in Japanese; English translation available from author)

Pearson CV, Rogers AD, Sheader M (2002) The genetic structure of the rare lagoonal sea anemone, *Nematostella vectensis* Stephenson (Cnidaria, Anthozoa) in the United Kingdom based on RAPD analysis. Mol Ecol 11:2285–2293

Ponder WF (1988) *Potamopyrgus antipodarum* – a molluscan coloniser of Europe and Australia. J Moll Stud 54:271–285

Prudhoe S (1985) A monograph on Polyclad Turbellaria. British Museum (Natural History), Oxford University Press, Oxford, England

Rabinowitz D, Cairns S, Dillon T (1986) Seven forms of rarity and their frequency in the flora of the British Isles. In: Soule ME (ed) Conservation biology: the science of scarcity and diversity. Sinauer Publishers, pp 182–204

Radashevsky VI, Hsieh H-L (2000) *Pseudopolydora* (Polychaeta: Spionidae) species from Taiwan. Zoological Studies 39:218–235

Raimondi PT (1992) Adult plasticity and rapid larval evolution in a recently isolated barnacle population. Biol Bull 182:210–220

Ricciardi A, Rasmussen JB (1998) Predicting the identity and impact of future biological invaders: a priority for aquatic resource management. Can J Fish Aquat Sci 55:1759–1765

Robins CR, Böhlke JE (1960) *Pikea sericea*, a synonym of the American centrarchid fish, *Micropterus salmoides*. Copeia 1960(2):147

Robinson TA, Griffiths CL, McQuaid CD, Rius M (2005) Marine alien species of South Africa – status and impacts. Afr J Mar Sci 27:297–306

Roller RA (1972) Three new species of eolid nudibranchs from the west coast of North America. Veliger 14:416–423

Rosenberg G (2005) Malacolog 4.0: A database of Western Atlantic marine Mollusca. [WWW database (version 4.0.2)] URL http://data.acnatsci.org/wasp

Rotramel G (1972) *Iais californica* and *Sphaeroma quoyanum*, two symbiotic isopods introduced to California (Isopoda, Janiridae and Sphaeromatidae). Crustaceana(Suppl)3:193–197

Roy MS, Sponer R (2002) Evidence of a human mediated invasion of the tropical western Atlantic by the "world's most common brittlestar." Proc R Soc London B 269:1017–1023

Russell FS (1953) The Medusae of the British Isles. Cambridge University Press, Cambridge

Saltonstall K (2002) Cryptic invasion by a non-native genotype of the common reed, *Phragmites australis*, into North America. Proc Natl Acad Sci 99:2445–2449

Sax DF, Stachowicz JJ, Gaines SD (eds) (2005) Species invasions. Insights into ecology, evolution, and biogeography. Sinauer, Sunderland, Massachusetts

Schaefer CT, Lewin J (1984) Persistent blooms of surf diatoms along the Pacific coast, USA. Mar Biol 83:205–217

Schuchert P (1996) Athecate hydroids and their medusae (Cnidaria: Hydrozoa). N Z Ocean Inst Mem 106

Schuchert P (2004) Revision of the European athecate hydroids and their medusae (Hydrozoa, Cnidaria): Families Oceanidae and Pachycordylidae. Rev Suisse Zool 111:315–369

Schwindt E (2007) The invasion of the acorn barnacle *Balanus glandula* in the south-western Atlantic 40 years later. J Mar Biol Assoc UK 87:1219–1225

Southward AJ, Burton RS, Coles SL, Dando PR, DeFelice RC, Hoover J, Parnell PE, Yamaguchi T, Newman WA (1998) Invasion of Hawaiian shores by an Atlantic barnacle. Mar Ecol Prog Ser 165:119–126

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. Smithsonian Contrib Zool 177:1–135

Stachowicz JJ, Whitlatch RB, Osman RW (1999) Species diversity and invasion resistance in a marine ecosystem. Science 286:1577–1579

Stachowicz JJ, Terwin JR, Whitlatch RB, Osman RW (2002a) Linking climate change and biological invasions: ocean warming facilitates nonindigenous species invasions. Proc Natl Acad Sci 99:15497–15499

Stachowicz JJ, Fried H, Osman RW, Whitlatch RB (2002b) Biodiversity, invasion resistance, and marine ecosystem function: reconciling pattern and process. Ecology 83:2575–2590

Stock JH (1968) Pycnogonida collected by the Galathea and Anton Bruun in the Indian and Pacific Oceans. Videnskabelige Meddelelser fra Dansk Naturhistorisk Forening 131:7–65

Stoddart HE, Lowry JK (2003) Zoological catalogue of Australia. Crustacea: Malacostraca: Peracarida: Amphipoda, Cumacea, Mysidacea. Volume 19.2B. CSIRO Publishing, Victoria, Australia

Strasser M (1999) *Mya arenaria* – an ancient invader of the North Sea coast. Helgolander Meeresuntersuchungen 52:309–324

Strathmann MF, Strathmann RR (2006) A vermetid gastropod with complex intracapsular cannibalism of nurse eggs and sibling larvae and a high potential for invasion. Pacific Sci 60:97–108

Straus SY, Lau JA, Carroll SP (2006) Evolutionary responses of natives to introduced species: what do introductions tell us about natural communities. Ecol Lett 9:357–374

Swennen C, Dekker R (1995) *Corambe batava* Kerbert, 1886 (Gastropoda: Opisthobranchia), an immigrant in the Netherlands, with a revision of the family Corambidae. J Moll Stud 61:97–107

Taiti S, Ferrara F (1986) Taxonomic revision of the genus *Littorophiloscia* Hatch, 1947 (Crustacea, Isopoda, Oniscidea) with descriptions of six new species. J Natl Hist 20:1347–1380

Taiti S, Howarth FG (1995) Terrestrial isopods from the Hawaiian Islands (Isopoda: Oniscidea). Occ Pap B P Bishop Mus 45:59–71

Torrey HB (1902) The Hydroida of the Pacific coast of North America. Univ Calif Publ Zool 1:1–104

Turner RD (1966) A survey and illustrated catalogue of the Teredinidae (Mollusca: Bivalvia). Museum of Comparative Zoology, Harvard Univ

Van Name WG (1936) The American land and fresh-water isopod Crustacea. Bull Am Mus Nat Hist 71:1–535

Van Name WG (1940) A supplement to the American land and fresh-water Isopod Crustacea. Bull Am Mus Natl Hist 77:109–142

Van Name WG (1945) The North and South American ascidians. Bull Am Mus Natl Hist 84:

Vervoort W (1964) Note on the distribution of *Garveia franciscana* (Torrey, 1902) and *Cordylophora caspia* (Pallas, 1771) in the Netherlands. Zool Mededel 39:125–146

Vine PJ, Bailey-Brock JH, Straughan D (1972) Spirorbinae (Polychaeta, Serpulidae) of the Hawaiian chain. Part 2, Hawaiian Spirorbinae. Pacific Sci 26:150–182

Walther AC, Lee T, Burch JB, Ó Foighil D (2006) Confirmation that the North American ancylid *Ferrissia fragilis* (Tryon, 1863) is a cryptic invader of European and East Asian freshwater ecosystems. J Moll Stud 72:318–321

Wasson K, Fenn K, Pearse JS (2004) Habitat differences in marine invasions of central California. Biol Invas 7:935–948

Watling L (1975) Remarks in: L. S. Kornicker, Spread of ostracodes to exotic environs on transplanted oysters. Bull Am Paleo 65:129–139

Williams AB (1984) Shrimps, lobsters, and crabs of the Atlantic coast of the eastern United States, Maine to Florida. Smithsonian Institution Press, Washington, D.C., 550 pp

Winston JE, Heimberg BF (1986) Bryozoans from Bali, Lombok, and Komodo. Am Mus Novit 2847:1–49

Wyatt T, Carlton JT (2002) Phytoplankton introductions in European coastal waters: why are so few invasions reported? In: CIESM (Commission Internationale pour l'Exploration Scientifique de la mer Mediterranée) Workshop Monographs no. 20, Monaco, pp 41–46

Wolff WJ (2005) Non-indigenous marine and estuarine species in The Netherlands. Zool Meded 79

Zabin CJ, Zardus J, Pitombo FB, Fread V, Hadfield MG (2007) A tale of three seas: consistency of natural history traits in a Caribbean-Atlantic barnacle introduced to Hawaii. Biol Invas 9:523–544

Zibrowius H (1971) Les especes méditerranéennes du genre *Hydroides* (Polychaeta, Serpulidae) remarques sur le pretendu polymorphisme de *Hydroides uncinata*. Tethys 2:691–746

Zimmerman EC (1948) Insects of Hawaii. Vol 3, Heteroptera. University of Honolulu Press, Honolulu